ZooKeys 14: 1-36 (2009)
doi: 10.3897/zookeys.14.188
www.pensoftonline.net/zookeys

RESEARCH ARTICLE

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Economically Beneficial Ground Beetles. The specialized predators *Pheropsophus aequinoctialis* (L.) and *Stenaptinus jessoensis* (Morawitz): Their laboratory behavior and descriptions of immature stages (Coleoptera, Carabidae, Brachininae)

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Academic editor: *Thorsten Assmann* | Received 25 April 2009 | Accepted 26 June 2009 | Published 10 July 2009

Citation: Frank JH, Erwin TL, Hemenway RC (2009) Economically Beneficial Ground Beetles. The specialized predators *Pheropsophus aequinoctialis* (L.) and *Stenaptinus jessoensis* (Morawitz): Their laboratory behavior and descriptions of immature stages (Coleoptera, Carabidae, Brachininae). ZooKeys 14: 1-36. doi: 10.3897/zookeys.14.188

Abstract

Adults of *Pheropsophus aequinoctialis* (L.) (Coleoptera, Carabidae, Brachininae, Brachinini), are largely nocturnal predators and scavengers on animal and plant materials. The daily food consumption of a pair of adults is the equivalent to 1.2-2.3 large larvae of *Trichoplusia ni* (Hübner) (Lepidoptera, Noctuidae). Larvae developed under laboratory conditions on a diet restricted to mole cricket eggs (Orthoptera, Gryllotalpidae); none survived under any other diet offered, thus they are specialists. Large numbers of brachinine eggs were laid in the laboratory, even on a paper towel substrate, and in all months of the year albeit with a strong suggestion of an annual peak in oviposition. Many eggs failed to hatch, but those that did so incubated an average 13.5 days. Many neonate larvae failed to feed and died. On average, the larvae that developed took 25.9 days to do so on an average 38.4 mole cricket eggs. The pupal period averaged 20.4 days, so the total developmental period was 59.9 days from oviposition to emergence of adult offspring at 26°C. After initial trials, an improved method of handling adults and rearing immature stages was developed, resulting in initiation of feeding by most neonate larvae and control of contaminating organisms (nematodes, mites, and Laboulbeniales). Most neonate larvae need to be in a cell or pit of sand (or earth) resembling a mole cricket egg chamber before they will feed on mole cricket eggs. The cause of infertility of many eggs was not resolved because it continued under the improved handling method for adults which permitted weekly mating; the presence of *Wolbachia* spp.

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(Bacteria: Rickettsiae) in the laboratory culture may be implicated. Sex ratios of emergent adults were not substantially different from 1:1.

Larvae of the Asian bombardier beetle *Stenaptinus jessoensis* (Morawitz) had been claimed in the literature to feed only on *Gryllotalpa* mole cricket eggs. We found they will feed on *Neocurtilla* and *Scapteriscus* mole cricket eggs in the laboratory. The behavior of *S. jessoensis* as adult and larva is very similar to that of *P. aequinoctialis* except that adults are mainly diurnal. Many of its eggs likewise are infertile. Many of its neonate larvae likewise were reluctant to feed. It, too, may have an annual peak in oviposition which alters under ambient laboratory conditions. Sex ratios of emergent adults were not substantially different from 1:1.

The structure of immature stages (eggs, larvae, and pupae) of *P. aequinoctialis* is contrasted with those of *S. jessoensis* and, in part, *Brachinus pallidus*.

Proof of restriction of the larval diet of *P. aequinoctialis* still is inadequate. Three *Scapteriscus* spp. are adventive pests in Florida, but *N. hexadactyla* (Perty) is a non-pest native species. This beetle might be used as a biological control agent in Florida if its larvae can be shown to cause great harm to *Scapteriscus* yet little or none to *Neocurtilla* mole crickets or other non-target organisms. It is conceivable this could be the case because of maternal care of eggs by *Neocurtilla* but not by *Scapteriscus*. However, the supporting research has not been done, mainly because of lack of a robust method for rearing *Neocurtilla*, under which maternal care and the fate of the eggs may easily be observed.

Keywords

Larvae, phylogenetic notes, diel behavior, mites, nematodes, Laboulbeniales, food, fecundity, fertility, prey specificity, Gryllotalpidae, biocontrol, *Wolbachia*

Introduction

The subtribe Pheropsophina is one of four subtribes of Brachininae (Coleoptera, Carabidae, Brachininae) (Erwin 1970, 1971; Lorenz 2005a, b). Pheropsophine bombardier beetles include only the Neotropical genus *Pheropsophus* Solier and its Eastern Hemisphere adelphotaxon *Stenaptinus* Maindron (Erwin 1971; Ball and Bousquet 2001).

Stenaptinus s. str. has 114 described species (Lorenz 2005a, b). There are descriptions of the first instar *S. hispanicus* (Dejean) (Emden 1919), and *S. africanus* (Dejean) (Boldori 1939). Habu and Sadanaga (1965, 1969) described and illustrated all three instars and a rearing method for *S. jessoensis* (Morawitz). The first instar is an active triangulin, the second and third instars are hypermetamorphic. The larvae develop only in real or simulated mole cricket egg chambers, only on a diet of *Gryllotalpa* mole cricket eggs. Experimental evidence for those statements was not provided by Habu and Sadanaga (1965, 1969). The adults are generalist predators, feeding on various insects, including pests, and ovipositing in June and July (Habu and Sadanaga 1965). In China, five artificial diets for overwintered female *S. jessoensis* were compared in terms of longevity of the beetles, egg production, egg fertility and incubation time; some of the artificial diets were almost as good as a diet of various insects on which each female produced 42.2 eggs, the last female survived until mid-July, 31.3% of eggs hatched, and mean incubation time was 12.3 days (Li 1988).

Pheropsophus s. str. has seven described species (Erwin 1970); however, a few others are as yet undescribed and numerous synonyms need to be checked; the genus is in need of a modern revision. The most widespread and markedly variable species, *P. aequinoctialis* (L.), has been reported from Argentina (Catamarca, Jujuy), Bolivia, Brazil, Costa Rica, Ecuador, Mexico (Yucatán), Nicaragua, Panama, Paraguay, Peru, Uruguay, and Venezuela (Erwin 2001). Adult *P. aequinoctialis* have a crepitating behavior like other Brachinini, producing quinones (Zinner et al. 1991) and they are nocturnal, running on sandy trails or riverine beaches, hiding during the day under stones, grass clumps, and drift logs and often in aggregations; they are predatory on other insects and also will eat some plant materials, such as ripe fruits of *Astrocaryum* sp., a palm (Reichardt 1971). Adult *P. aequinoctialis* feed on adult *Scapteriscus* mole crickets in sand-filled containers in the laboratory (A. Silveira-Guido, pers. comm.). Adult *P. rivieri* (Demay) inhabit seasonally-inundated floodplains in the Amazon drainage of Brazil, and share the water banks with *Scapteriscus* mole crickets; dissections of females revealed that the reproductive period is confined to the first three months of falling water levels (Zerm and Adis 2003). Immature stages of *Pheropsophus* have heretofore not been described, and we do that here.

We compared food consumption and diel behavior of adults of *S. jessoensis* and *P. aequinoctialis*, their oviposition, fertility of eggs, and development time of immature stages, and contrasted the results of feeding the larvae on various diets. We describe the immature stages of *P. aequinoctialis* and contrast them with those of *S. jessoensis*, which we also redescribed in part, here. Notes are also provided about structural attributes of the larvae of *Brachinus* in contrast to those of *Pheropsophus* and *Stenaptinus*. Although *Brachinus* has no conceived biocontrol importance, recent knowledge about the ecology and behavior of its species (Juliano 1983, 1984, 1985a, b, 1986a, b, c; Saska and Honek 2004) is useful for comparative purposes.

Materials and methods

A culture of the pest mole cricket *Scapteriscus abbreviatus* Scudder has been maintained by the University of Florida/Institute of Food and Agricultural Sciences' Mole Cricket Research Program since the 1980s. The stock was initially collected by pitfall traps in Broward County, Florida. Rearing methods are to be described by S.A. Wineriter, now with USDA-ARS, Gainesville, FL, who did much to develop them. This is an ideal mole cricket to rear because it is multivoltine, thus enabling production of eggs year-around. It may be reared without restriction in Florida because, although it is non-native, populations are established. Its shipment to other parts of the USA would need USDA-APHIS permit because it is a "plant pest" which is subject to restriction of interstate shipping. Maintenance is labor-intensive, but survival is high. As necessary for the work below, *Sc. borellii* Giglio-Tos, *Sc. vicinus* Scudder, and *Neocurtilla hexadactyla* (Perty) were captured in Alachua County, FL and reared by the same methods to produce eggs. Those species are all univoltine in northern Florida, so eggs are avail-

able only for a few weeks of each year. Their survival in culture was poorer or, for *N. hexadactyla*, much poorer than for *Sc. abbreviatus*.

We initiated cultures of the house cricket *Acheta domesticus* (L.) (Orthoptera: Gryllidae) and the mealworm *Tenebrio molitor* (L.) (Coleoptera: Tenebrionidae). We obtained eggs of *Gryllus* sp. (Orthoptera: Gryllidae) from T. J. Walker, and eggs and larvae of *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) from a USDA-CMAVE culture. These, and cucumber slices were offered to the beetle larvae as alternative diets. Raisins and oatmeal, offered to adult beetles, and also cucumber, were from a grocery store in Gainesville, FL.

A shipment of *Stenaptinus jessoensis* adults was made from southern Japan in 1986 (Y. Tanaka, Kobe City, and Y. Yahiro, Yoshida). Importations of *P. aequinoctialis* were made from: Departamento de Rivera, Uruguay in 1986 (A. Silveiro-Guido, Montevideo, Uruguay), Montero, Bolivia in 1987, 1988, and 1992 (C.J. Pruett, Santa Cruz, Bolivia, sometimes with assistance from F.D. Bennett, Univ. Florida), 1988, Rio Grande do Norte, Brazil (K. Zinner, Universidade de São Paulo, Brazil), 1989, São Paulo de Potenji, Rio Grande do Norte, Brazil (J.H. Frank). Cultures initiated were maintained separately according to collection locality, and in quarantine at the Florida Biological Control Laboratory, Gainesville, FL. All the *Pheropsophus* adults that we imported proved to be *P. aequinoctialis sensu lato*.

Laboratory behavior of adults

A pair of wild-caught adult *P. aequinoctialis* was held in each of 10 plastic boxes, 31 cm L × 23 cm W × 10 cm H, filled to × 5 cm with moistened sand, initially sterile, from July through October 1986. Additional moisture was provided by deionized water-soaked cotton in a small Petri dish embedded in the sand surface. A triple thickness of non-sterile moist paper towel, 8 × 23.5 cm, was provided on the surface as a shelter. Five large *Trichoplusia ni* larvae were provided as food in each box. At daily check for 4 months, these larvae were counted; missing or dismembered larvae were noted and the number was increased again to five living larvae, and any that had begun to spin cocoons were replaced. Dismembered larvae were removed. Daily for 10 days, the location of each adult beetle was noted as in the open on the surface, under a piece of paper towel, or in a self-constructed burrow. Pairs of *S. jessoensis* were treated simultaneously and identically.

First instars (planidia) of both species were sometimes noticed on the sand surface, so oviposition was occurring. Eggs could not be seen on the sand surface, so would have to be extracted from the sand by a flotation method, or the beetles would have to be induced to oviposit on a more artificial substrate, before they could be documented. Remains of *T. ni* larvae attracted phorid flies. Phoretic organisms that had arrived with the adult beetles were not being suppressed. For these reasons we developed a more artificial and sterile handling method.

We developed a rearing method in which adults were housed in small groups on crumpled, moist, brown paper towel in 237 ml (8 fl. oz.) plastic "deli" cups with press-on lids. Some females were housed solitarily in 150 ml cups for some recording needs. Paper towel served as oviposition substrate. Once eggs had been removed, the paper towel was autoclaved together with any contaminating organisms. Survival of adults was good and eggs were readily found. Our routine removed these "egg papers" weekly (but daily for some recording needs) and transferred the beetles into transparent plastic boxes, 31 cm L × 23 cm W × 10 cm H, with fresh paper towel and food. As food, we provided *T. molitor* pupae, oatmeal, and raisins, all of which were observed to be fed upon. After a 2-day exposure to this food, beetles were placed once again in plastic "deli" cups, and the remaining contents of the feeding containers were autoclaved. Feeding containers and plastic cups were washed and dipped in ~ 5% bleach. Although the diet we developed was not perfected by trials, it was adequate because the adults survived well and normally produced many eggs each week. We wore eye protection when handling adult beetles because they are well able to aim their defensive spray toward human eyes. Our fingers became stained by their defensive secretions unless we wore gloves.

Oviposition

Eggs produced by field-caught females confined solitarily in 150 ml plastic cups with crumpled, moist paper towel were harvested daily from June 1986 through May 1987 for *S. jessoensis*. One female (no male) was in each cup. Each was removed from its cup once weekly for one day to another cup where it was confined with a large *T. ni* larva. At first the beetles were in a room with natural window light supplemented by overhead fluorescent lights only when people were working there. In January 1987, we were required to move them to another room with little illumination because of space shortage, but there we operated overhead fluorescent lights for 9 h/d. Temperature in the building was constant at 26°C. The frequency (eggs/female/day) was recorded during February 1987, for a total of 145 eggs observed.

Similar records for *P. aequinoctialis* likewise produced a frequency distribution, but the period of observation was continued until early April until 145 eggs had likewise been tabulated. Eggs were transferred by fine artist's paintbrush from "egg papers" to discs of brown paper towel, two layers, in small Petri dishes, ~ 5 cm diam. × 1 cm H. These were examined daily and moistened with a fine spray of water from a wash bottle. Neonate larvae were transferred by fine artist's paintbrush to individual containers. We were surprised by the large number of eggs produced and by the large number of infertile eggs, which eventually molded or collapsed.

Egg fertility

For 10 days from 8 July 1986, the viability of the first 10 eggs from each of 10 field-collected *S. jessoensis* females was recorded.

We observed low fertility of eggs in *S. jessoensis* and *P. aequinoctialis*. Because the bacterial genus *Wolbachia* may cause cytoplasmic incompatibility in many insects (Werren 1997), we asked A. Jeyaprakash (see Jeyaprakash and Hoy 2000) to test our *P. aequinoctialis* for the presence of *Wolbachia*. On confirmation of its presence, we tried to eliminate it from our laboratory culture in hope this would lead to increased fertility of eggs. In an effort to kill the *Wolbachia*, part of the culture was housed at 35°C for 24 hours, whereas the remaining part was left untreated.

Initiation of larval feeding

At first, for both beetle species, we placed neonate larvae into small plastic Petri dishes (≈ 5 cm diameter × 1 cm height) stocked with mole cricket eggs on moist paper towel, in the expectation that mole cricket eggs might serve as diet. Survival was very poor: most larvae roamed for their entire life span (see below), frequently walking over the eggs, but did not feed, and then died. We offered instead eggs of *T. ni*, pieces of *T. ni* larvae, eggs of *Gryllus* sp., and small pieces of cucumber. The few larvae that did begin to feed would almost invariably survive and develop, but only on a diet of mole cricket eggs. We enclosed the Petri dishes in aluminum foil to exclude light, to no avail. We filled the Petri dishes with sand except for a shallow central depression, to no avail. We tried using plenty (30) of mole cricket eggs from the outset because of a suggestion by Habu and Sadanaga (1965, 1969) that larvae could recognize that small numbers were inadequate for their development, and refuse to feed, to no avail. We speculated that initiation of feeding relied upon dual cues of burrowing through sand and consequent arrival at mole cricket eggs, so we devised columns of sand of various depths up to 30 cm in Plexiglas® tubes over plastic chambers containing mole cricket eggs on paper towel. None of this improved initiation of feeding so it is not reported in detail.

Ultimately, we adopted a variant of the method used by Habu and Sadanaga (1969) for rearing *S. jessoensis*. They used real and artificial mole cricket eggs chambers constructed with mud. We placed sand into a plastic vial (4 cm diameter × 6.5 cm height) to a depth of ~ 5 cm. An "artificial mole cricket egg chamber" was scooped from the sand. Mole cricket eggs (≥30) were placed into the chamber, and the top of the chamber was covered with broken pieces of wooden tongue depressors, which were covered by more sand. Then, a neonate larva was dropped onto the sand surface. Usually, it then burrowed to the eggs, fed on them, and developed to the adult stage. The method worked well, but it denied us the ability to observe attack by the neonate larva on the eggs and subsequent development. Much later, by accident and after the culture of *S. jessoensis* had been terminated, we discovered that the egg chambers do

not have to be covered to exclude light: many larvae will develop without this step. This allowed some observation of development of the larvae, although they had to be observed at the bottom of a pit ~ 2 cm deep; the small larvae were difficult to see among a pile of mole cricket eggs.

Larval and pupal development

By using records from individuals that survived when reared in plastic Petri dishes under daily observation, we compared development times of the F_1 immature stages of *S. jessoensis* and *P. aequinoctialis* when larvae were provided with a diet of mole cricket eggs. We obtained specimens of the developmental stages of *P. aequinoctialis* and *S. jessoensis* for taxonomic description.

Tests of larval prey specificity

We compared survival of *P. aequinoctialis* on various diets, albeit initially under inadequate conditions, and later in pits in sand within vials.

Optimization of diet

When we had learned to build artificial mole cricket egg chambers in which to present a diet to neonate larvae, and the number of mole cricket eggs they needed, we tried to minimize that number of eggs without sacrificing survival.

Descriptions of immature stages

Bousquet and Goulet (1984) provided a code of notation for primary "ancestral" setae and pores for carabid beetle larvae based on a study of 78 species representing 20 tribes. Erwin and Medina (2003) amplified that system in their description of the first known larva of the carabid tribe Ctenodactylini. We have followed this descriptive system herein and provide additional enhancements to the coding protocols particularly in reference to the hypermetamorphic stages of brachinine beetles. In the Bousquet and Goulet (1984) coding system, the following apply to the illustrations provided herein: as (anterior sclerite); cc (coxal cavity); g (preceding capital letters of sclerite code signifies setal group); pt (prosternite); ss (abdominal sternal sclerites); sa (spiracle); AN (antenna); CO (coxa); EG (egg buster tooth); EM (epimeron); EP (epipleurite); ES (episternum); EY (eye spot); FE (femur); FR (frontale); LA (labium); ME (mesonotum and metanotum); MN (mandible); MS (mesosternum and metasternum); MX (maxilla); PA (parietale); PL (pleurite); PR (pronotum); PS (prosternum); PY (pygidium); ST (sternites

and sterna sclerite of abdomen); TA (tarsus); TE (tergite of abdominal segments); TI (tibia); TR (trochanter); TS (trochantin); UH (urogomphal hooks); UN (claw); UR (tergite of abdominal segment IX and urogomphi); I-X (abdominal segments).

In most cases, setae are numbered on the left side of illustration and pores are lettered on the right side of illustration according to their ancestral positions (Bousquet and Goulet 1984); additional setae and pores are numbered and lettered sequentially beyond that presented in Bousquet and Goulet (1984), where appropriate.

Habu and Sadanaga (1965, 1969) were the first to describe in detail the immature stages of *Stenaptinus jessoensis* (Morawitz), at about the same time Erwin (1967) described in detail the immature stages and way of life of the new world species *Brachinus pallidus* Erwin. Below, we will briefly compare and contrast immature stages of *Brachinus* with our newly described immature stages of *Pheropsophus aequinoctialis* (Linné) and *Stenaptinus jessoensis* (Morawitz).

Results

Field behavior of *P. aequinoctialis* adults

Notes provided by our collectors give hints on the habitat of adult *P. aequinoctialis*. All collectors agree with Reichardt (1971) that they are nocturnal and are most readily collected with the aid of a flashlight, while they are moving at night. In Brazil, they were seen at night on sandbars in Amazonian rivers (K. Zinner), running at night among clumps of grasses by an artificial pond providing water to cattle (J.H. Frank), in Uruguay, running on the soil surface (A. Silveira-Guido), in Bolivia, on a riverbank, often under driftwood or stranded dead fish during the day (F.D. Bennett and C.J. Pruett). In the western Amazon Basin, they are nocturnal on the alluvial and sandy banks of large rivers (Fig. 1) running together with the tiger beetles *Phaeoxantha aequinoctialis* (Dejean) and *P. klugii* (Chaudoir) and the galeritine carabid beetle *Trichognathus marginipennis* Latreille, all of which share similar coloration and color pattern, likely forming a Mullerian mimicry complex (Erwin 1991).

Parasites and phoretics of adults

Many of the field-collected adult *Pheropsophus* were infested with nematodes, mites, and Laboulbeniales. Nematodes and mites were provided to specialists who told us they were non-pathogenic. Smart and Nguyen (1994) described a new species of *Rhabditis* (Nematoda: Rhabditidae), and H.A. Denmark (pers. comm.) identified a large mite (*Echinomegistus* sp., Paramegistidae) from beetles from Potenji. Other mites remained unidentified. Pinned adult beetles retain specimens of Laboulbeniales, which we will provide upon request to specialists. Use of the revised rearing methods suppressed these contaminants.

Figure 1. Riverine beach habitat of *P. aequinoctialis* along the Río Madre de Dios watershed, Peru (Photo credit: T.L. Erwin).

Laboratory behavior of adults

A direct contrast between the two species showed large differences in diel behavior. Although it has been stated that adult *P. aequinoctialis* are nocturnal, this is not entirely true (Table 1).

Mean daily food consumption by pairs of *P. aequinoctialis* fell from 2.34 *T. ni* larvae in July to 1.23 in October. In comparison, that of *S. jessoensis* fell from 2.27 in July to 0.99 in October (Table 2).

Table 1. Dispersion of adult *P. aequinoctialis* and *S. jessoensis* in sand-filled boxes observed daily in late morning averaged over 10 consecutive days. Twenty boxes each contained a pair of wild-caught beetles of one of the two species. The 20 adults of each species were recorded as being (a) in the open, (b) sheltering under a triple thickness of paper towel, or (c) by default, in a self-constructed burrow. SD = standard deviation of mean.

Species	***P. aequinoctialis***			***S. jessoensis***		
	Open	Shelter	Burrow	Open	Shelter	Burrow
Mean	3.3	0.2	16.5	13.9	4.8	1.3
SD	2.2	0.4	1.9	3.8	3.2	1.1

Table 2. Mean daily consumption of large *T. ni* larvae by pairs of wild-caught adult beetles over the months July-October 1986, based on 10 pairs of each species housed by pair in sand-filled boxes. SD = standard deviation of mean.

Species	***P. aequinoctialis***				***S. jessoensis***			
Month	Jul	Aug	Sep	Oct	Jul	Aug	Sep	Oct
Mean	2.34	1.58	1.51	1.23	2.27	1.47	1.22	0.99
SD	0.58	0.44	0.46	0.39	0.43	0.63	0.48	0.38

Oviposition

The number of eggs produced per female by field-caught *S. jessoensis* declined from June-July 1986, but by November had once more begun to increase, and in February-March 1987 was at least as high as it had been at the outset (Table 3).

The 31 adult female *S. jessoensis* were of unknown age when received in June. About half of them survived at least a year. Average monthly oviposition by the surviving group had declined to 0 by September, but then it increased somewhat, and increased much more after hours of artificial lighting were increased in January, and by March was at least as great as it had been at the outset. The initial June-July oviposition matches the report (Habu and Sadanaga 1965, 1969) of annual oviposition in those months, but the observed increase in oviposition beginning in November and peaking in February-March does not do so; perhaps the increase in illumination in January 1987 advanced it. We learned that oviposition is not confined to June-July. If there is one annual ovipositional peak as suggested by Habu and Sadanaga (1965, 1969) and Li (1988), its timing changes under ambient conditions.

Despite constant laboratory conditions, the number of eggs laid per female per day varied from one to 31 (Fig. 2).

The major difference from the trial with *S. jessoensis* is that only fertile eggs, those from which larvae eventually hatched, were recorded. Many infertile eggs were produced but are not recorded. These females were brought to observation from the southern hemisphere autumn at the end of April and were immediately exposed to a northern hemisphere daylight regime. Then, the apparent peak of oviposition was in January. However, females laid fertile eggs during every months of the year. They were of unknown age when recording began.

Table 3. Numbers of eggs laid monthly by wild-caught *S. jessoensis* females from June 1986 to May 1987. N = number of surviving *S. jessoensis* females at end of month, mean = mean number of eggs laid by survivors, SD = standard deviation of mean.

Month	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**
N	31	29	28	28	28	28	27	24	23	21	17	16
Mean	53	32	3	0	<1	12	12	11	54	70	34	3
SD	39	35	9	0	2	32	31	35	56	63	47	7

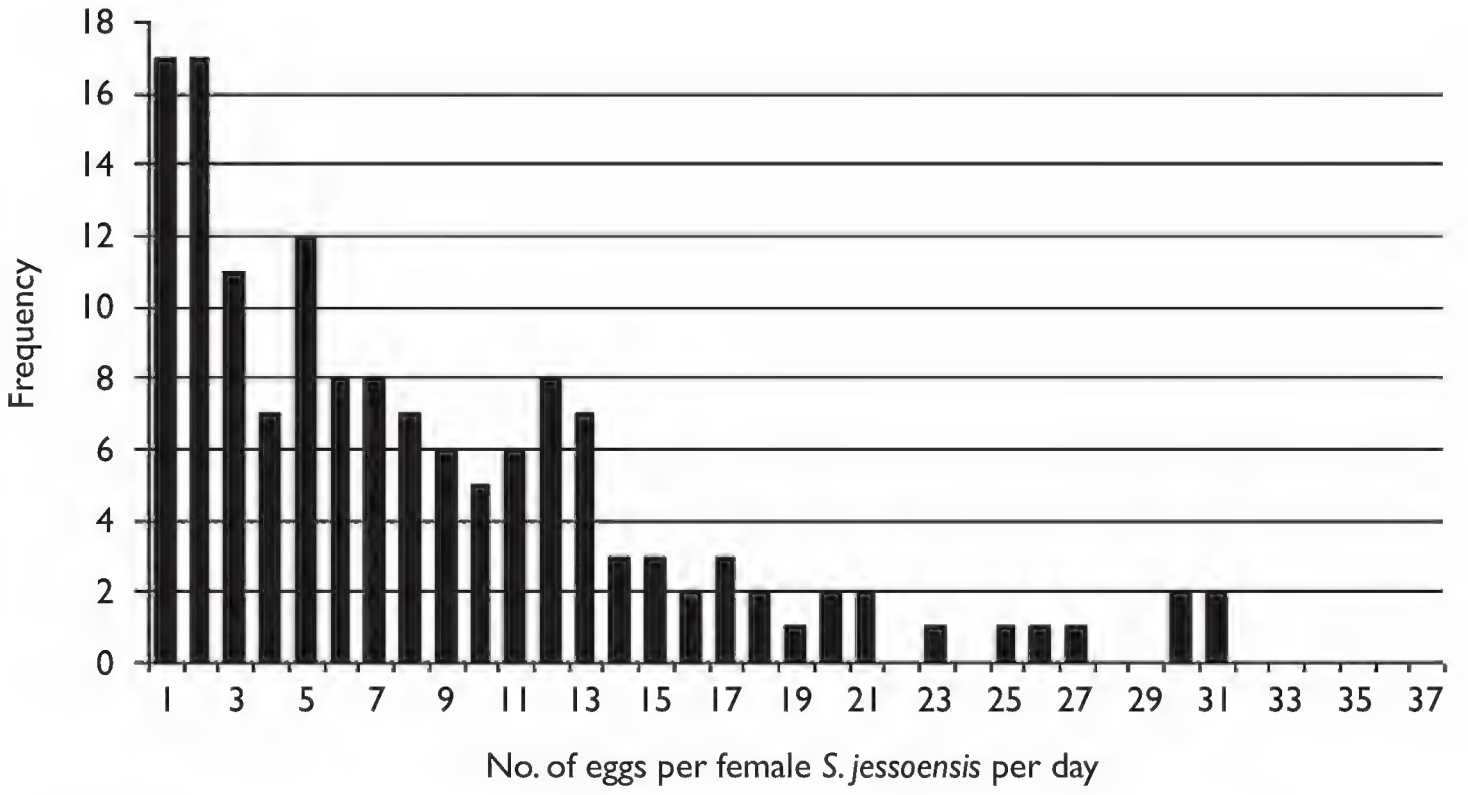


Figure 2. Frequency of numbers of eggs laid daily by *S. jessoensis* females in February 1987 (Σ observations = 145 excluding records of zero).

Just as with *S. jessoensis*, the number of eggs laid daily by female *P. aequinoctialis* varied (Fig. 3). Although the number 5, and perhaps harmonics of it (10, 15, 20) in Fig. 3, and perhaps Fig. 2, has a high frequency, we can think of no biological explanation, and we assume this occurred by chance. Most eggs were laid singly, but some were clustered in groups. Group sizes ranged up to 13 for *S. jessoensis*, up to 17 for *P. aequinoctialis*; these group sizes, too, may occur by chance.

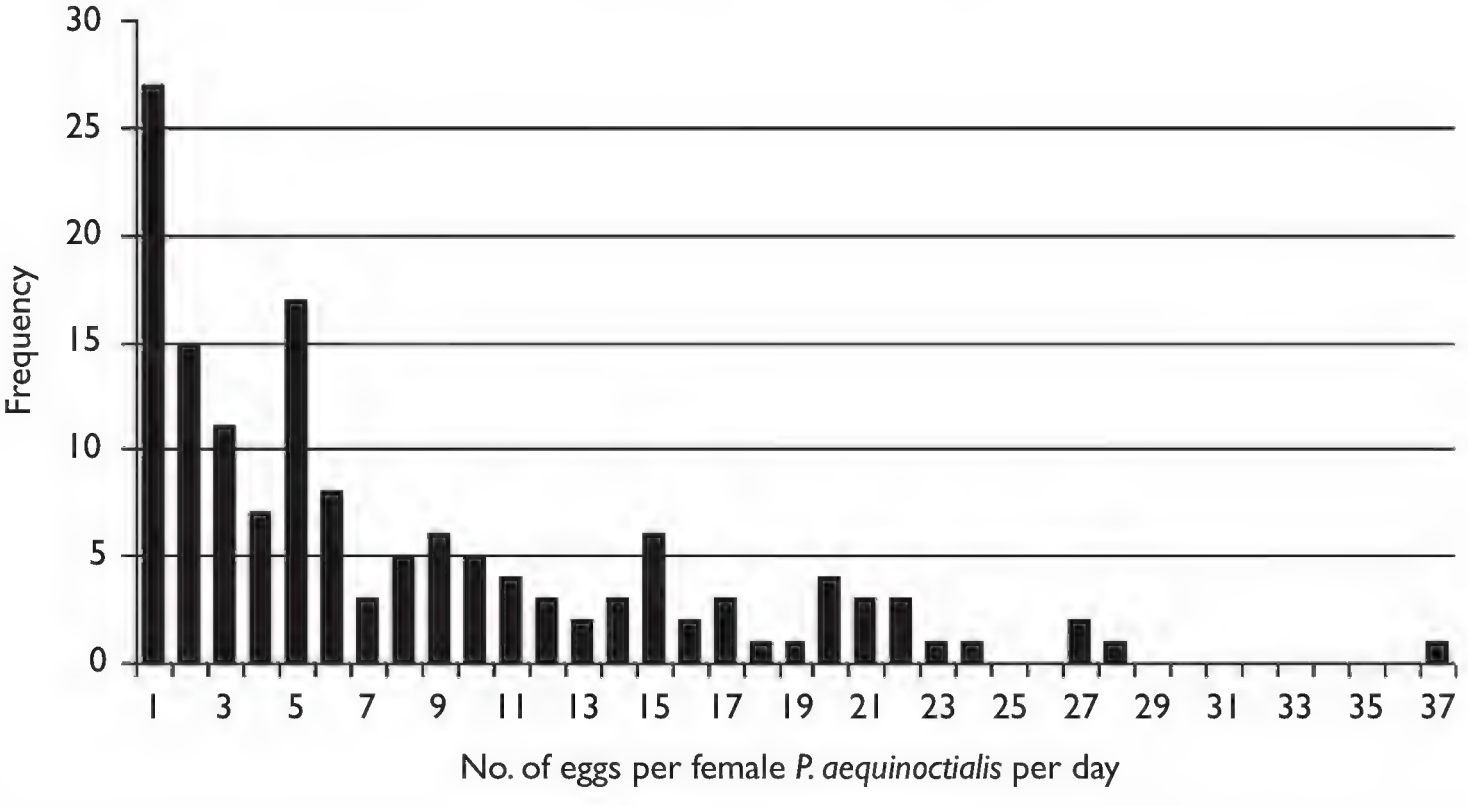


Figure 3. Frequency of numbers of eggs laid daily by *P. aequinoctialis* females in February-April 1987 (Σ observations = 145 excluding records of zero).

Egg fertility

The number of eggs produced (fecundity) fluctuated widely. Furthermore, fertility of eggs was often low but fluctuated widely. Fertility had no obvious relation to season, nor would we necessarily have expected a relationship to season because rearing was carried out under constant temperature and light. Fluctuations sometimes resulted in absence of hatchling larvae from our culture, but the longevity of the adults and their resumption of oviposition of fertile eggs prevented loss of the culture.

Wolbachia bacteria were present in our *P. aequinoctialis* culture (A. Jeyaprakash, pers. comm.). Raising the temperature to a sublethal level has been known to eliminate *Wolbachia* from other insects (Werren 1997). We briefly explored this possibility. Our attempt to improve the proportion of fertile eggs, by eliminating bacteria, by raising the ambient temperature of an incubator in which part of the culture was housed at 35°C for 24 hours was unsuccessful. This heat treatment of adult beetles resulted in total cessation of oviposition for several weeks. When they began to oviposit again, they still produced a large proportion of infertile eggs.

After oviposition, by day 8 the pigmented larval mandibles are visible through the thin chorion of viable eggs.

Initiation of larval feeding

Presentation to neonate larvae of eggs of *T. ni*, pieces of *T. ni* larvae, eggs of *Gryllus* sp., and small pieces of cucumber on paper towel in small Petri dishes seemed to elicit no feeding response except to pieces of cucumber. Neonate larvae were observed to imbibe liquid from cucumber, but then they blackened and died. Only mole cricket eggs elicited a feeding response, and only sometimes, that led to development of larvae to the pupal stage. Dozens of trials failed because not even the control treatment, mole cricket eggs, was successful.

Larval and pupal development times

Pheropsophus aequinoctialis had shorter development in instar I and longer in the pupal stage, and it consumed more prey eggs relative to *S. jessoensis* (Table 5). Eggs of all four mole cricket species were used as diet for *S. jessoensis*, and the species offered seemed to make no difference in development time. Survival of *P. aequinoctialis* was achieved only on eggs of *N. hexadactyla* and *Sc. borellii*, but this was because of the poor experimental conditions; subsequent routine rearing on *Sc. abbreviatus* eggs shows they are an adequate diet; again the specific identity of the eggs did not seem to influence development time.

Table 4. Numbers of eggs laid monthly by 10 wild-caught *P. aequinoctialis* females from late April 1987 to March 1988. They were housed solitarily in plastic cups with crumpled paper towel, and were given access to one large *T. ni* larva per week as prey. N = number of surviving *P. aequinoctialis* females at end of month, mean = mean number of fertile eggs laid by survivors, SD = standard deviation of mean.

Month	Apr+May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
N	10	10	10	10	10	9	9	9	8	5	2
Mean	12	2	2	2	2	3	5	5	21	9	4
SD	22	5	7	6	6	7	8	9	29	6	6

Table 5. Development times in days of immature *S. jessoensis* and *P. aequinoctialis* when F_1 neonate larvae were provided with eggs of *Neocurtilla hexadactyla*, *Scapteriscus abbreviatus*, *Sc. borellii,* or *Sc. vicinus* at 26°C. TL = total larval period, TD = Total duration of immature stages, Food = number of mole cricket eggs consumed, SD = standard deviation of mean.

	Egg	Inst I	Inst II	Inst III	TL	Pupa	TD	Food
***S. jessoensis*, n = 12, of which 7 males, 5 females**								
Mean	11.4	11.6	4.7	15.2	29.7	15.1	56.0	23.0
SD	0.5	2.2	1.2	3.3	3.6	0.3	3.5	5.1
***P. aequinoctialis*, n = 11, of which 2 males, 4 females, 5 not recorded**								
Mean	13.5	6.7	4.4	14.8	25.9	20.4	59.9	38.4
SD	1.7	1.6	2.0	1.5	2.3	2.1	2.0	11.5

Tests of larval prey specificity

Initiation of feeding by neonate larvae was largely unsuccessful until arenas were changed from Petri dishes to artificial mole cricket egg chambers.

A count at 14 days showed no survivors on the diet of *T. molitor* pupae, but almost all of the latter decomposing; this suggests that the neonate *P. aequinoctialis* had injured the mealworm pupae. When, in an immediate add-on trial, 10 *T. molitor* pupae were placed into such cells without *P. aequinoctialis* larvae, eight survived to the adult stage; the other two molded, supporting that viewpoint. A count at 14 days showed no more than one survivor in each cell initially supplied with two larvae; this suggests fratricide, because at that point numerous prey eggs remained.

Tests were also conducted to detect whether *P. aequinoctialis* larvae, having developed to instar II on *Sc. abbreviatus* eggs, could be switched to *P. molitor* pupae and would develop. If successful, this could lead to reduced rearing costs. Twenty five artificial egg chambers were constructed. Into each were placed 5 *Sc. abbreviatus* eggs and one neonate *P. aequinoctialis* larvae. After 5 days, 11 beetle larvae were alive in instar II, the uneaten mole cricket eggs in each chamber were removed and replaced with one *T. molitor* pupa. None of the beetle larvae survived to the adult stage.

Another set of tests used 30 artificial mole cricket egg chambers. Thirty *Sc. abbreviatus* were placed into each of 10, 100 *Acheta domesticus* eggs were placed into each of 10, and a

tiny cube of cucumber weighing 0.2 g was placed into each of 10. The piece of cucumber was replaced at day 7. A check for surviving beetle larvae was made at day 14, at which time there were eight survivors, and all of them had been provided with *Sc. abbreviatus* eggs.

Among the various diets provided, only mole cricket eggs proved adequate.

Optimization of diet

To optimize the number of mole cricket eggs required for larval development, we provided 24, 27, or 30 *Sc. abbreviatus* eggs, expecting that the lower numbers of eggs would affect the number of survivors and/or pupal weight, and this would determine an optimal diet in terms of success vs resources.

Not all of the eggs provided were eaten by all of the survivors, indicating that at least a diet of 30 eggs is adequate. Although such diet (30 eggs) may not provide the fastest rate of growth or the largest pupae, it is adequate for development, and it conserves resources (mole cricket eggs). In Table 6, we found that 7 of 10 larvae survived when presented with 30 *Sc. abbreviatus* eggs. In the current test, 12 larvae (of 20) survived when presented with 30 eggs (6 of 10), or 15 (of 20) (7.5 of 10) survived when presented with 27 eggs – there is no significant difference. However, when presented with only 24 eggs, only 7 of 20 (3.5 of 10) larvae survived. We were expecting reduced survival at reduced diet, and analyzed this as a 1-tailed χ^2 test with Yates' correction for small numbers, and found a significant difference (7/20 vs 14/20, $\chi^2 = 3.61$, df =1, $P<0.05$, 1-tailed). There was a positive trend of effect of diet on resultant pupal weight. Thus, a diet of 24 eggs is suboptimal, and a diet of ≥ 30 eggs is better, at least in terms of resultant pupal weight, which may influence reproductive success of resultant

Table 6. Survival to adult stage of *P. aequinoctialis* when neonate larvae were provided with a diet of 30 *Sc. abbreviatus* eggs or one *T. molitor* pupa in an artificial mole cricket egg chamber.

No. of larvae in cell	Diet provided	No. cells	No. alive at 14 d	No. surviving to adult	Sex of ensuing adults
One	30 *Sc. abbreviatus* eggs	10	7	7	3♂, 4♀
Two	30 *Sc. abbreviatus* eggs	10	8	8	4♂, 4♀
Two	1 *T. molitor* pupa	10	0	0	n.a.

Table 7. Numbers surviving (out of 20 neonate larvae) and pupal weights of *P. aequinoctialis* when provided with 24, 27, or 30 *Sc. abbreviatus* eggs. SD = standard deviation of mean.

Diet presented	24 eggs	27 eggs	30 eggs
Number of survivors	7	15	12
Mean pupal weight (g)	0.2266	0.2450	0.2621
SD	0.0207	0.0194	0.0143

adults, and also in terms of survival. The standard length of an adult *P. aequinoctialis* in our culture was about 16.6 mm, whereas adults produced under restricted larval diet were as small as 10.4 mm.

Taxonomic treatment

Stenaptinus jessoensis (Morawitz)

Egg (Fig. 4). White. Rectangulate with moderately rounded apices. Surface with numerous small perforations; micropore ill-defined, slightly raised.

Instar I. Form. (Fig. 5) Campodeiform planidium; head relatively large compared to prothorax, eyes absent. Frontale with single-tooth egg-burster near base of head on frontale. Body markedly setiferous throughout dorsally; regular fixed setae ventrally. Segment X (PY): sternite (Figs. 5, 13) with two large serrated recurved teeth, serrations on distal margin and with seta PY7 markedly long, stout and curved posteriorly. Urogomphi (Figs. 12, 13) each a small fleshy blunt knob with numerous spicules. These are not well illustrated in Habu and Sadanaga (1969, p. 176).

Coloration. Mostly white color with slightly creamy-colored head capsule and apical abdominal segments; mandibles slightly darkened toward the tips.

Chaetotaxy. *Head.* (Figs. 6, 7) Frontale (Fig. 6) with 8 setae (FR1 – FR5, FR7, FR10 – FR11; FR6 replaced by pore, FR8 & FR9 missing) and 6 pores (FRa – FRf) each side. Parietale (Figs. 5, 6, 7) with 31 setae (PA1 – PA31) and 17 pores (PAa – PAr; pore e absent) each side. Antenna (Figs. 5, 6): antennomere 1 with 4 pores (ANa – ANd); antennomere 2 with 3 pores (ANh – ANj); antennomere 3 with 3 setae (AN1 – AN3), no pores, and 2 small sensilla near apex of sensorial appendage (Fig. 6); antennomere 4 with 4 setae (AN4 – AN7) and 1 pore (ANg) and 2 small apical sensilla (Figs. 5, 6). Mandible (Figs. 5, 6) with 1 seta (MN1) and 3 pores (MNa – MNc). Labium (Fig. 7): prementum with 2 setae (LA1 – LA2) and 1 pore (LAa) on each side ventrally; palpomere 1 with 1 pore (LAb); palpomere 2 and 3 without pores. Maxilla (Figs. 5, 7): cardo partially fused with stipes, with 1 seta (MX1); stipes with 6 setae (MX2 – MX7) and 3 pores (MXa – MXc), MX6 articulated; lacinia (Fig. 7) with 2 setae (MX7, MX9); galeomere 1 with 1 seta (MX10) and one pore (MXd); galeomere 2 with neither setae or pores; galeomere 3 with one pore (MXg); maxillary palpomeres without visible sensory features.

Thorax. Prothorax: Notum (Figs. 5, 8) with 14 major "ancestral" setae (PR1 – PR14) and numerous auxiliary setae (not labeled), PR1 absent, and 12 pores (PRa – PRl) on each side. Epimeron (Fig. 5) with 1 seta (PL1), and 2 pores (PLa – PLb) on each side. Episternum (Fig. 5) with 1 seta (ES1) and no pores. Trochantin (Fig. 9) with 5 setae (TS1 – TS5). Prosternite (Fig. 9) with 1 seta (PS1), gPS present with 3 setae and 2 pores each side.

Mesothorax and *metathorax*: Notum (Figs. 5, 8) with 14 "ancestral" setae (ME1 – ME14), numerous auxiliary setae (not labeled), and 7 pores (MEa – MEg) on each

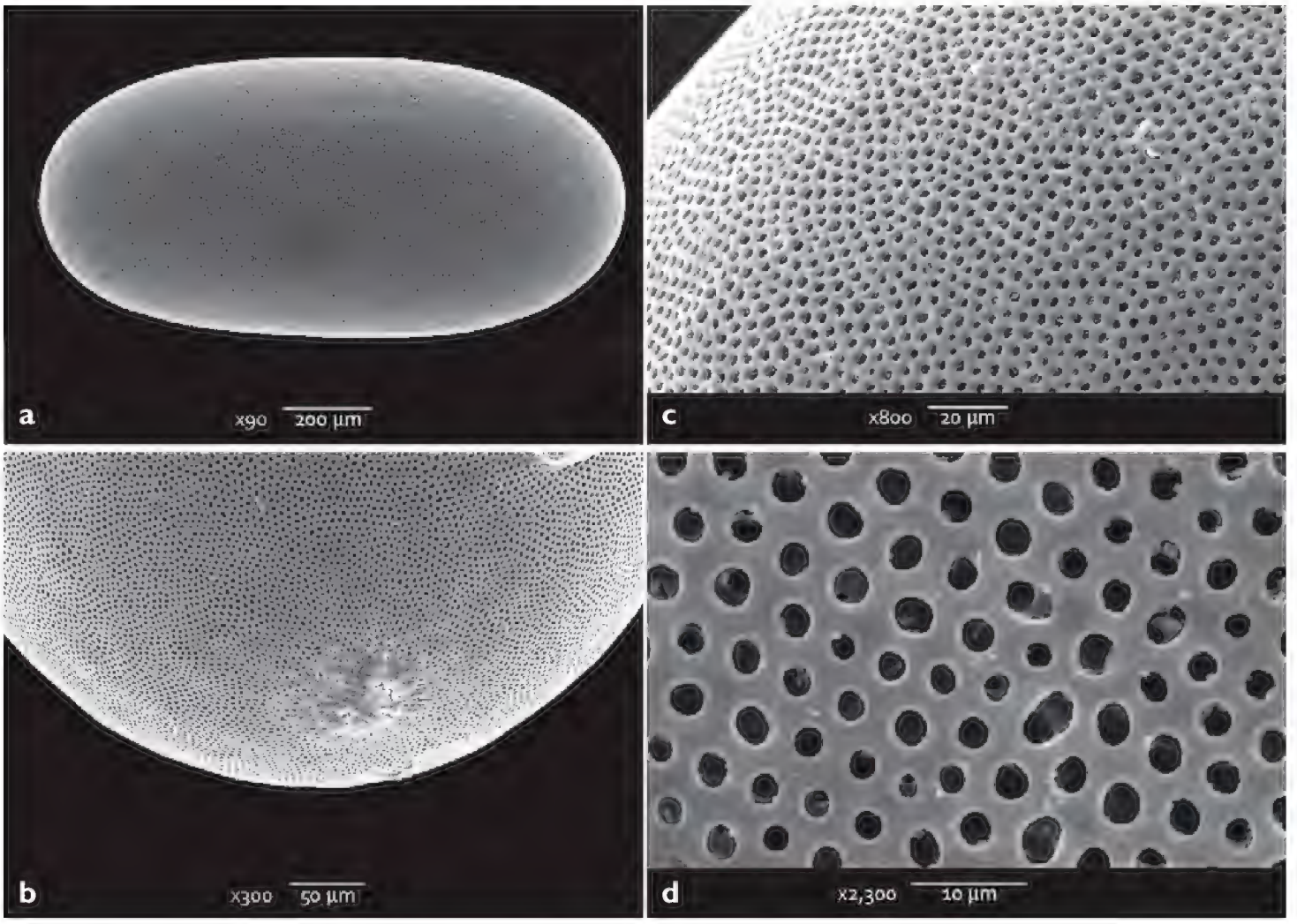


Figure 4. Scanning Electron Micrograph of egg of *S. jessoensis*: a, complete egg; b, apical micropore; c, surface texture; d, microperforations.

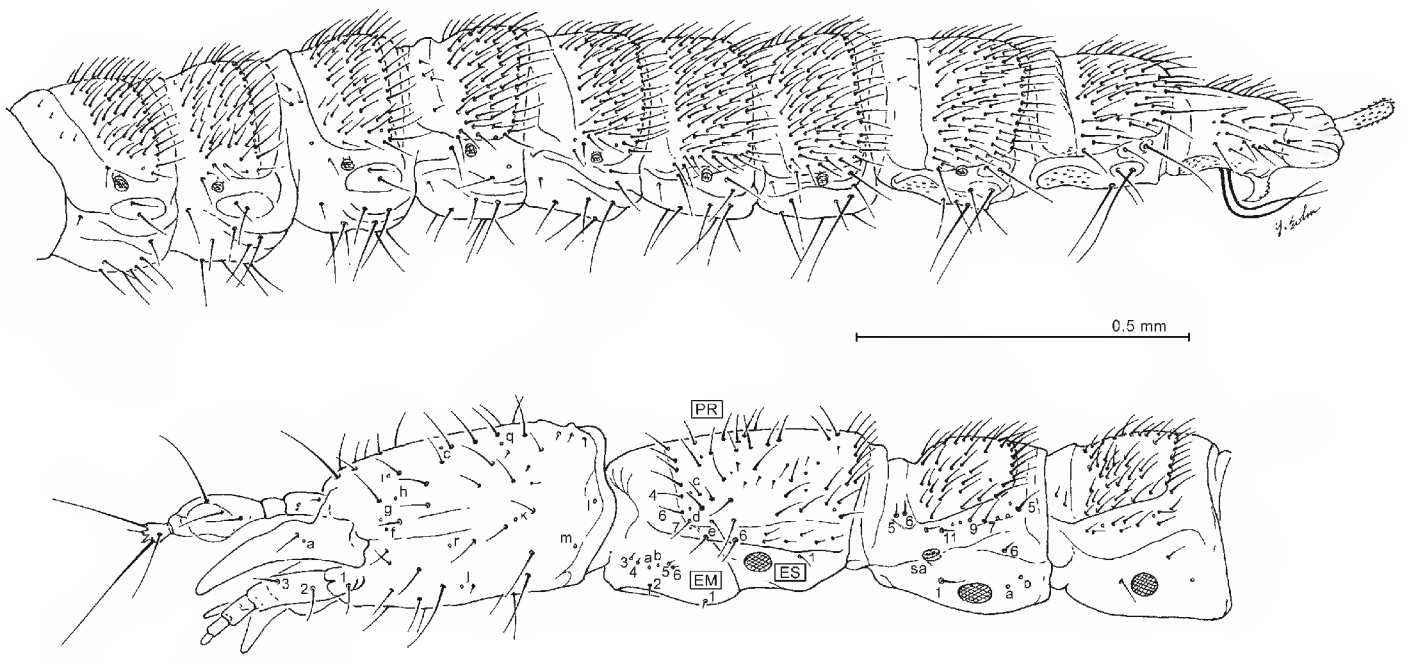


Figure 5. Habitus (left lateral aspect) of *S. jessoensis*, first instar; legs not shown.

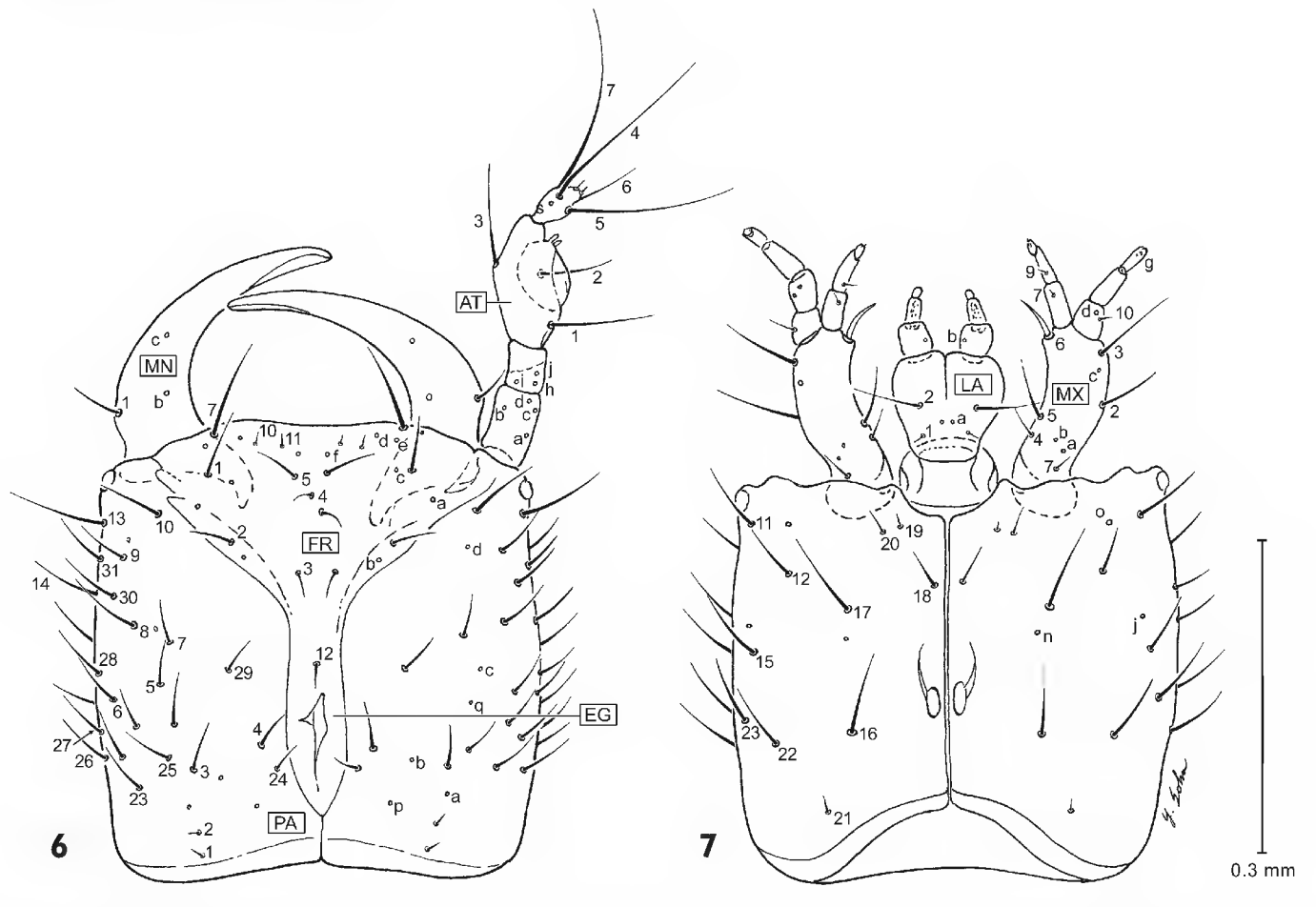
side. Episternum (Fig. 9) with 3 setae (ES1, ES5, ES6) and no pores. Trochantin (Fig. 9) with 5 setae (TS1– TS5). Epimeron (Fig. 9) with 1 seta (EM1). Sternum (Fig. 9) with 1 seta (MS1) each side.

Abdomen. Figs. 5, 10, 11, 12, 13. Tergite I (Fig. 5, 10) with 10 "ancestral" setae (TE1 – TE10) and numerous auxiliary setae (not labeled), and 3 "ancestral" pores (TEb – TE d) and 5 auxiliary pores (not labeled) each side. Tergites II – VIII as in Tergite I. Tergite IX, X and urogomphi (Fig. 12), IX with 4 setae (UR1 – UR4) and no pores. Epipleurite IX (Fig. 12) with 2 setae (EP1 – EP2) and no pores. Hypopleurite VII (Fig. 12) with 2 setae (HY1 – HY2) and no pores. Segment VII sternite (Fig. 13) with 5 setae (ST1 – ST5) each side and no pores. Segment IX sternite (Fig. 13) with 3 setae (ST1 – ST3) each side and no pores. Segment X (PY) sternite (Fig. 13) with 1 markedly arcuate seta (ST1) each side, no pores. Medially with two close-spaced serrated and recurved teeth (Figs. 5, 13).

Legs. (Fig. 14). All legs stout, similar in proportions and setation; anterior leg (top) slightly shorter than middle and posterior (bottom) ones. Coxa with 9 setae (ancestral CO1 – CO17, with CO1-6, 15, 16 absent, and 7 pores (COa-c, e-h, f-h not ancestral). Trochanter with 8 setae (TR1 – TR8) and no pores. Femur with 6 setae (FE1 – FE6) and 2 pores FEa and FEb. Tibia with 6 setae (TI1 and TI3 – TI7) with TI2 absent, and no pores. Tarsus with 1 constant seta (TA1) and one pore. Claws simple, with no setae or tooth, symmetrical in shape and size.

Instar III. Form. Hypermetamorphic stage 3rd instar (see Habu and Sadanaga, 1965, for description and illustrations).

Pupa. Not described.

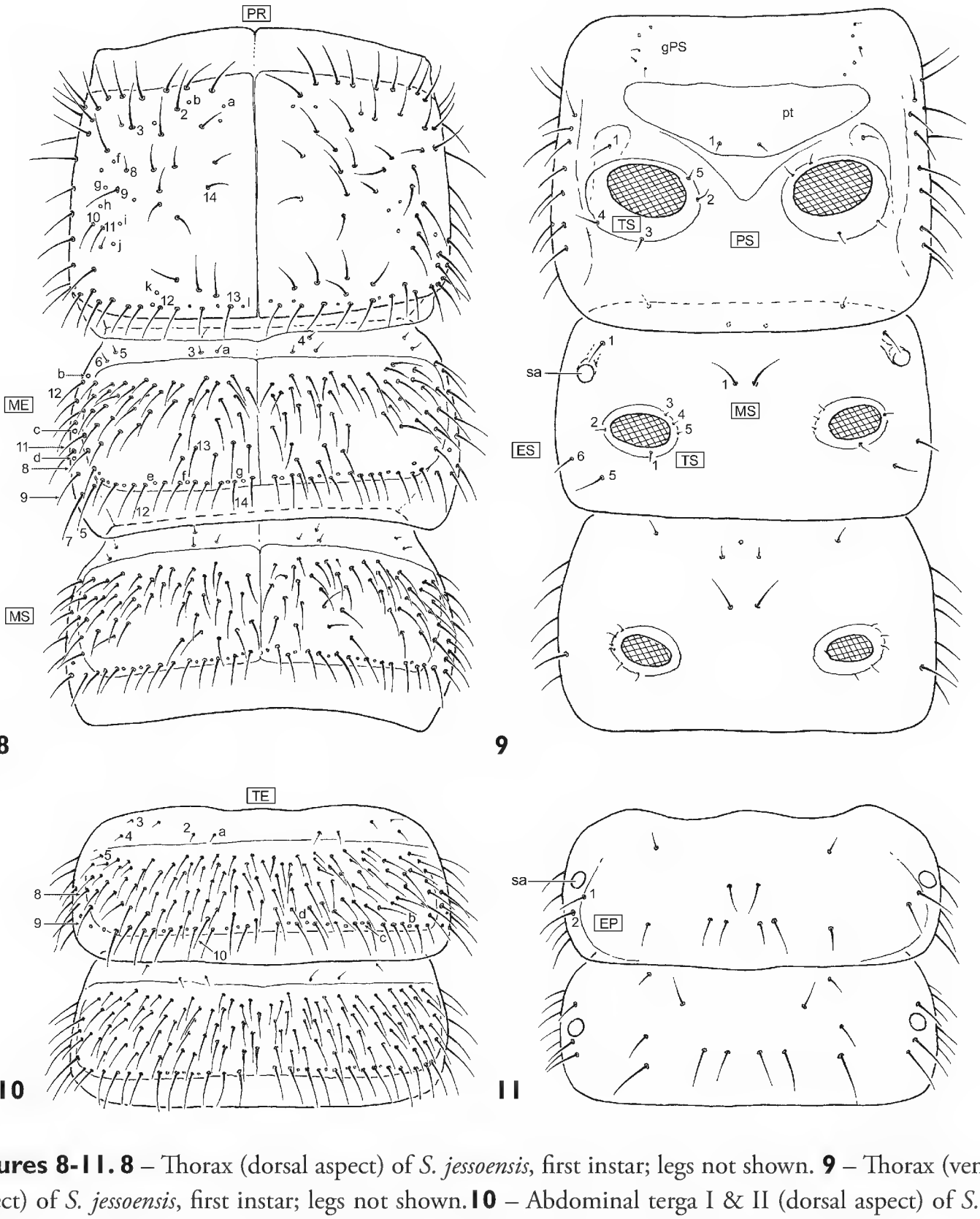


Figures 6-7. 6 – Head (dorsal aspect) of *S. jessoensis*, first instar; ventral mouthparts and left antenna not shown. **7**- Head (ventral aspect) of *S. jessoensis*, first instar; mandibles and antennae not shown.

Pheropsophus aequinoctialis (Linné)

Egg (Fig. 15). White. Rectangulate with moderately rounded apices. Surface polygonic, with numerous very close-spaced large perforations; micropore not obvious.

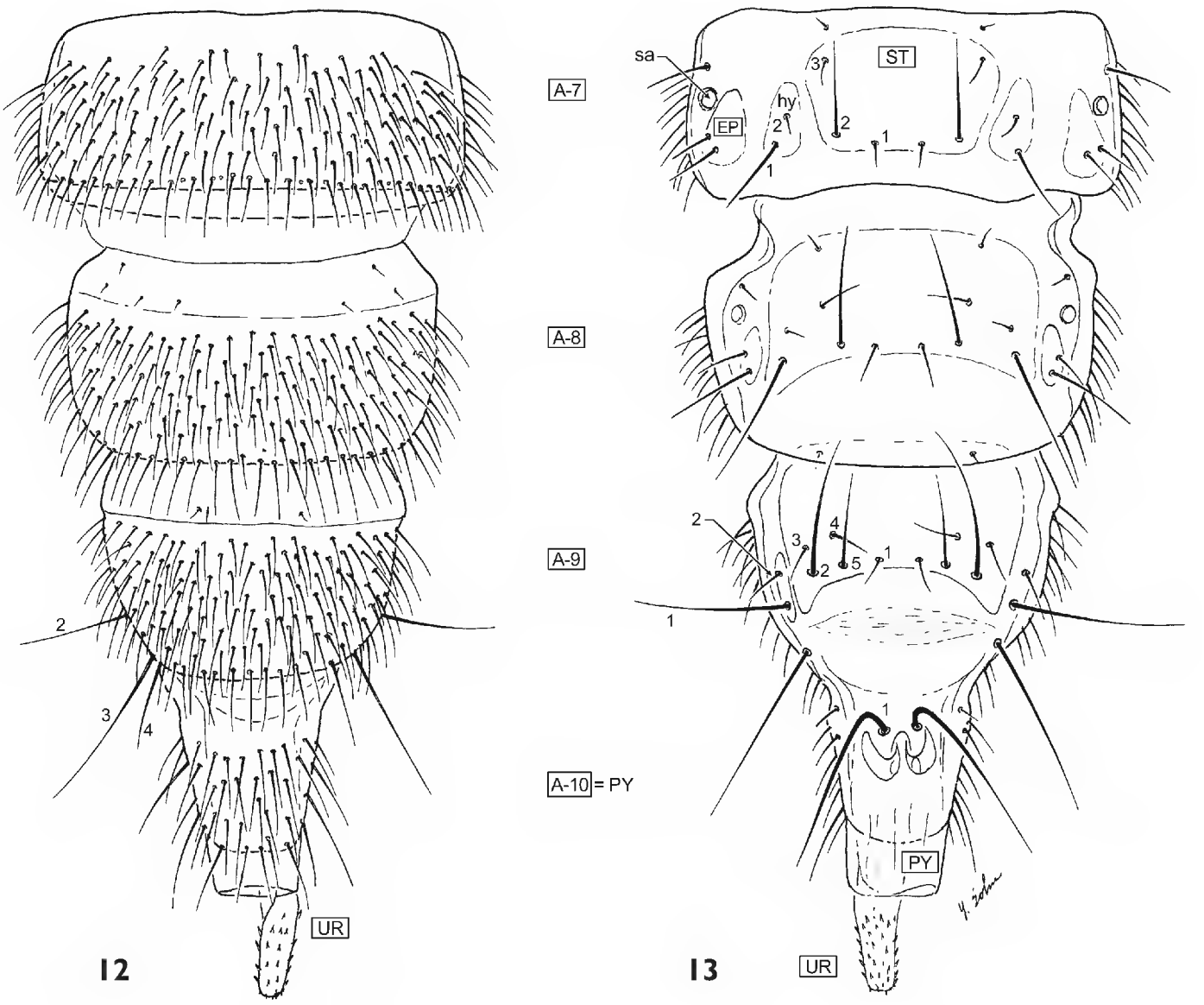
Instar I. Form. (Fig. 16) Campodeiform planidium; head relatively small compared to prothorax, eyes absent. Frontale with three simple-tooth egg-bursters near base of head on frontale. Body setiferous dorsally, less so than in *Stenaptinus* (see above). Segment X (PY): sternite (Figs. 16, 24) medially with two widely spaced non-serrated recurved teeth and with seta PY7 normal. Urogomphi (cf. Fig. 16) absent.



Figures 8-11. 8 – Thorax (dorsal aspect) of *S. jessoensis*, first instar; legs not shown. **9** – Thorax (ventral aspect) of *S. jessoensis*, first instar; legs not shown. **10** – Abdominal terga I & II (dorsal aspect) of *S. jessoensis*, first instar. **11** – Abdominal sterna I & II (ventral aspect) of *S. jessoensis*, first instar.

Coloration. Mostly white color with creamy-colored head capsule and slightly rufescent mandibles darkened toward the tips.

Chaetotaxy. *Head.* (Figs. 16, 17, 18) Frontale (Fig. 17) with 9 "ancestral" setae (FR1 – FR9, FR10 and 11 missing), and one auxiliary seta each side, and 2 pores (FRd – FRe, a, c, and f missing) left side, right side devoid of pores in specimen illustrated. Parietale (Figs. 16, 17) with 18 setae (PA1 – PA18) and 8 pores (PAa – PAl; pores d, f, g, h absent) each side. Antenna (Figs. 16, 17): antennomere 1 with 5 "ancestral" pores (ANa – ANe) and one auxillary pore (unlabeled); antennomere 2 absent or fused with 3; antennomere 3 with 3 "ancestral" setae (AN1 – AN3), one auxillary seta, and 1 pore (ANf), plus a dome-shaped hyaline sensillum; antennomere 4 with 4 setae (AN4 – AN7) and 1 auxillary seta, no pores, and 2 small apical sensilla. Mandible (Fig. 17) falciform without setae and pores. Labium (Fig. 18): prementum with 1 seta (LA3) and 1 pore (LAa) each side; palpomere 1 with 1 seta and 3 pores, none of which correspond to the "ancestral" schema; palpomere 2 with 1 apical sensillum. Maxilla (Fig. 18): cardo without setae; stipes with 5 "ancestoral" setae (MX1 – MX5), and 2 pores



Figures 12-13. 12 – Abdominal terga VII to X (dorsal aspect) of *S. jessoensis*, first instar. **13** – Abdominal sterna VII to X (ventral aspect) of *S. jessoensis*, first instar.

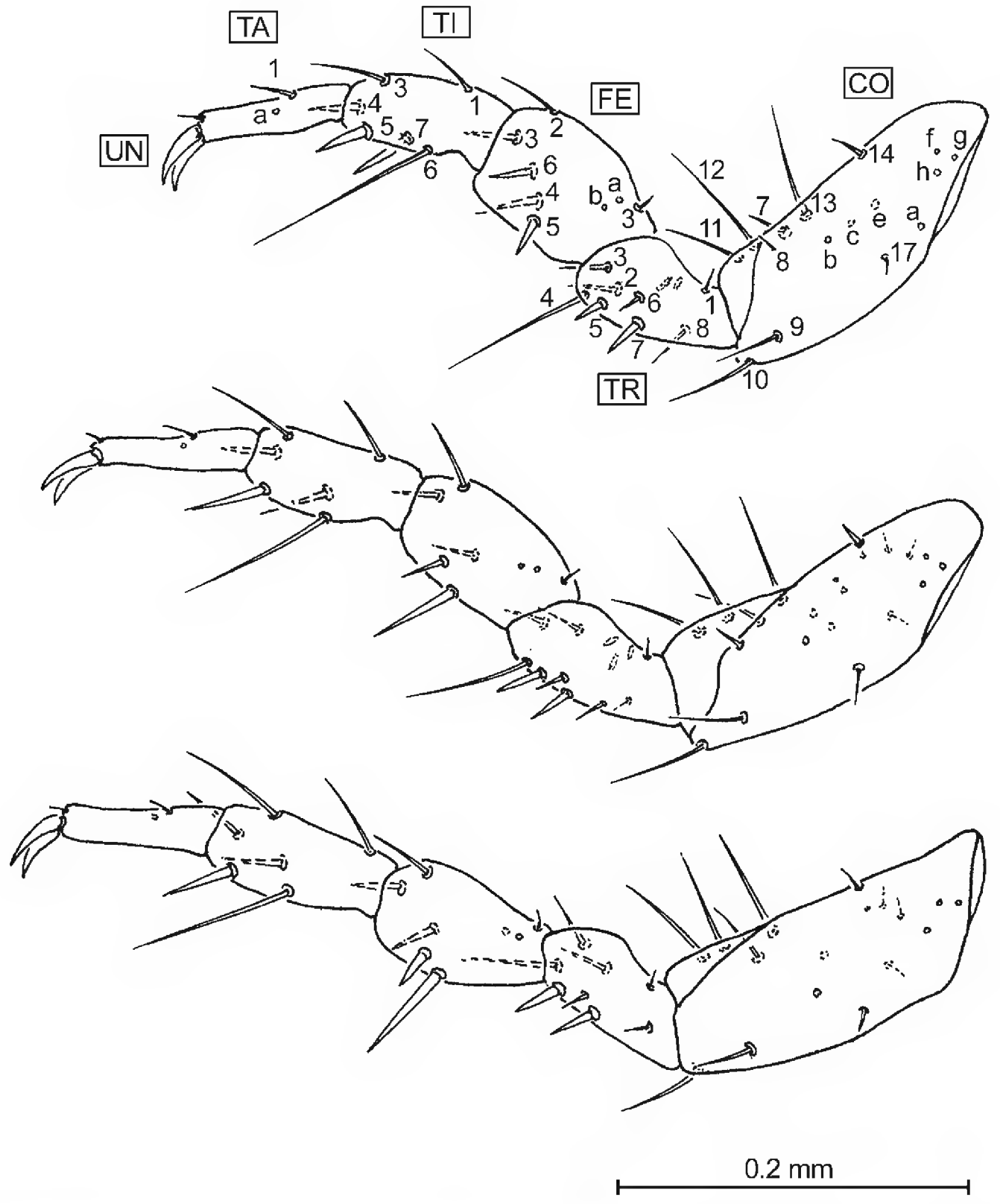


Figure 14. Legs (dorsal aspect, left side of thorax) of *S. jessoensis*, first instar. Top, anterior leg; middle, middle leg; bottom, posterior leg.

(MXa – MXb), and no variable setae (gMX) on dorsal side; lacinia (Fig. 18) with 1 seta (MX10); galeomere 1 with 1 seta (MX7) and no pores; galeomere 2 with 2 minute dorsal setae, no pores; maxillary palpomeres without visible sensatory features.

Thorax. *Prothorax*: Notum (Figs. 16, 19) with 1 identifiable major "ancestral" seta (PR9) and numerous auxiliary setae (not labeled), PR1 absent, and no pores. Epimeron (Fig. 20) with 1 seta (EP1), and no pores. Episternum and trochantin not defined. Prosternite (Fig. 20) with 1 seta "ancestral" (Pt1) and one auxiliary seta; gPS absent.

Mesothorax and *metathorax*: Notum (Figs. 16, 19, 20) with 1 identifiable major "ancestral" seta (PR9) and numerous auxiliary setae (not labeled), PR1 absent, and no pores. Mesepisternum (Fig. 20) with 2 setae (ES1, ES2) and no pores. Trochantin and epimeron not defined. Mesoprosterite (Fig. 20) with 3 setae (Pt1, Pt2, Pt3) each side; metaprosternite with 3 setae (Pt1, Pt2, Pt3). Metepisternum with 3 setae (ES1, ES2, ES4).

Abdomen. Figs. 16, 21-24. Tergite I (Figs. 16, 21) with possibly one "ancestral" seta (TE2) and numerous auxiliary setae (not labeled), and no pores. Tergites II – VIII as in

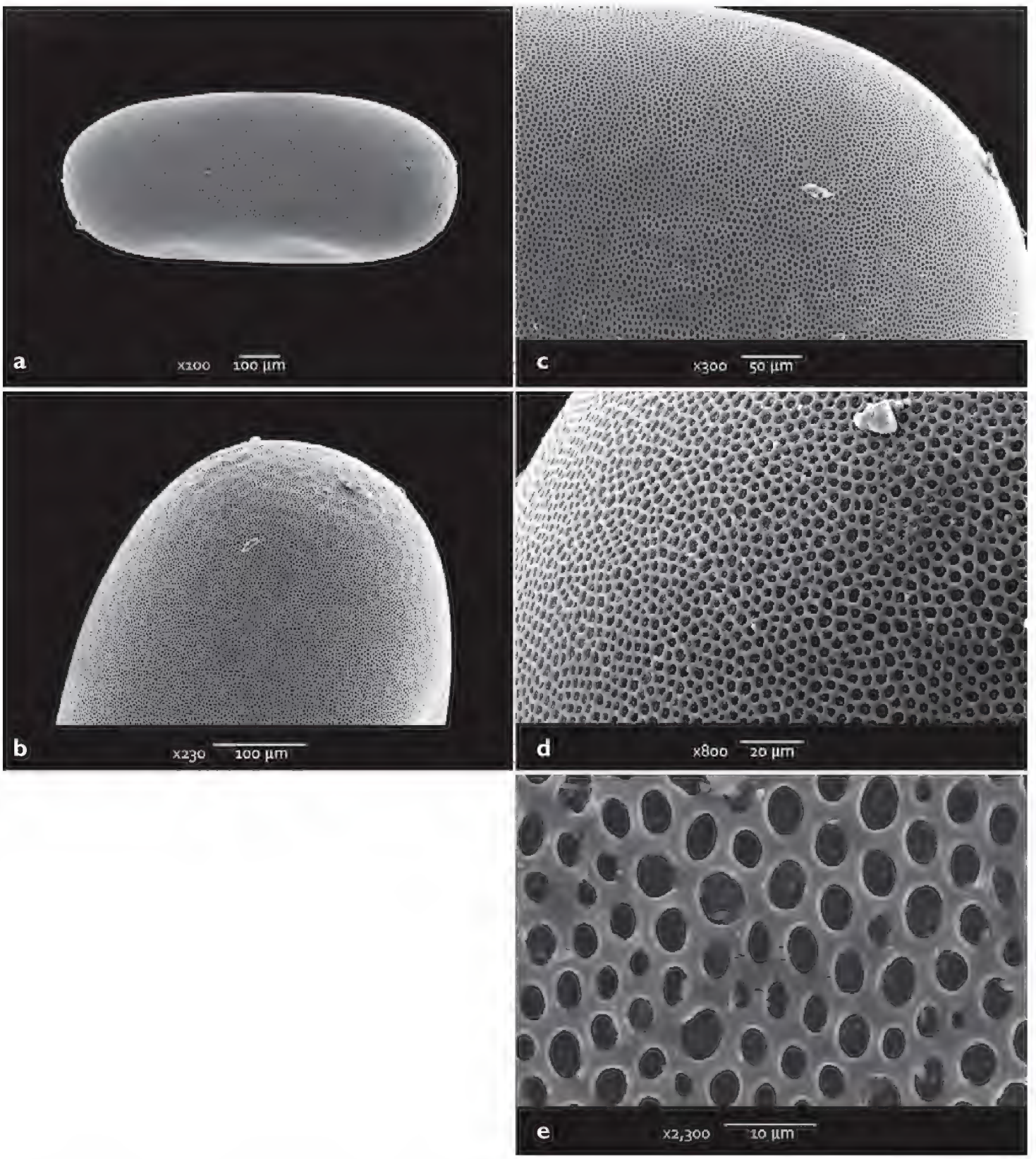


Figure 15. Scanning Electron Micrograph of egg of *P. aequinoctialis*: a, complete egg; b, apical aspect showing polygonical relief; c, surface texture; d, microperforation distribution; e, microperforations.

Tergite 1. Tergite IX, X and urogomphi (Figs. 16, 23), IX with 4 setae (UR8 – UR11) and no pores. Epipleurite IX (Fig. 16) with 2 setae (EP1 – EP2) and no pores. Hypopleurite VII (Fig. 16) with 2 setae (HY1 – HY2) and no pores. Segment VII sternite (Fig. 24) with 5 setae (ST1 – ST5) each side and no pores. Segment IX sternite (Fig. 24) with 3 setae (ST1 – ST3) each side and no pores. Segment X (PY) sternite (Figs. 16, 24) with 1 seta (ST1) each side, no pores. Medially with two wide-spaced non-serrated and recurved teeth (Figs. 16, 24).

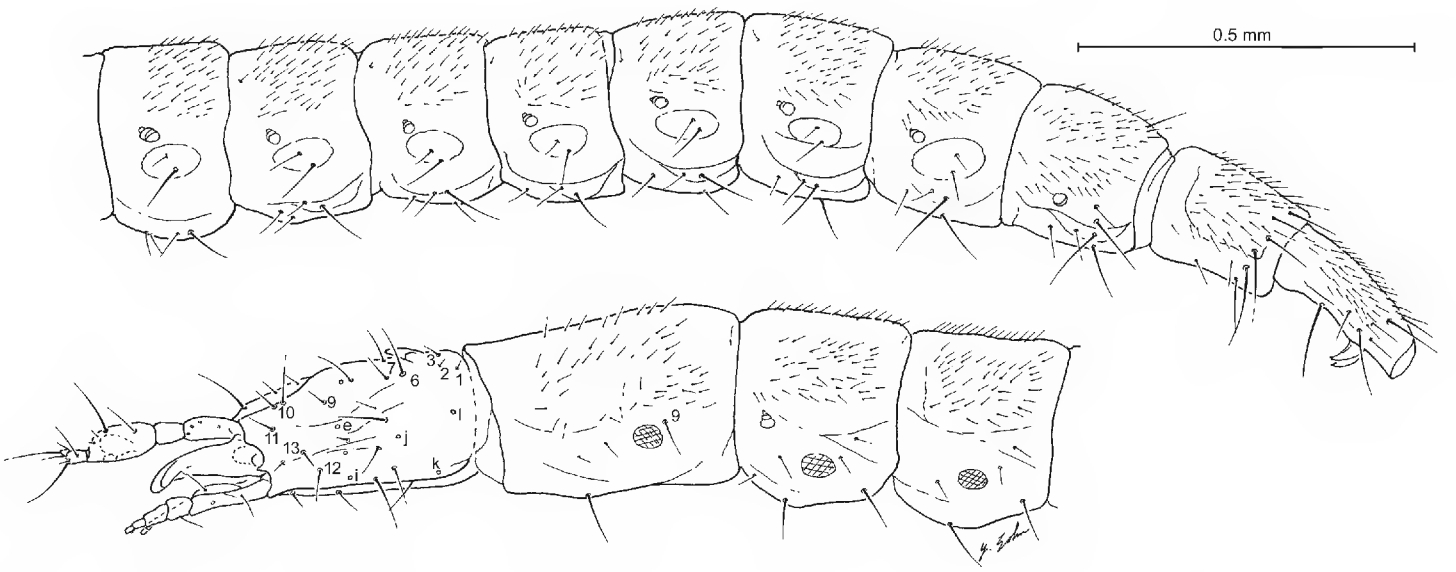
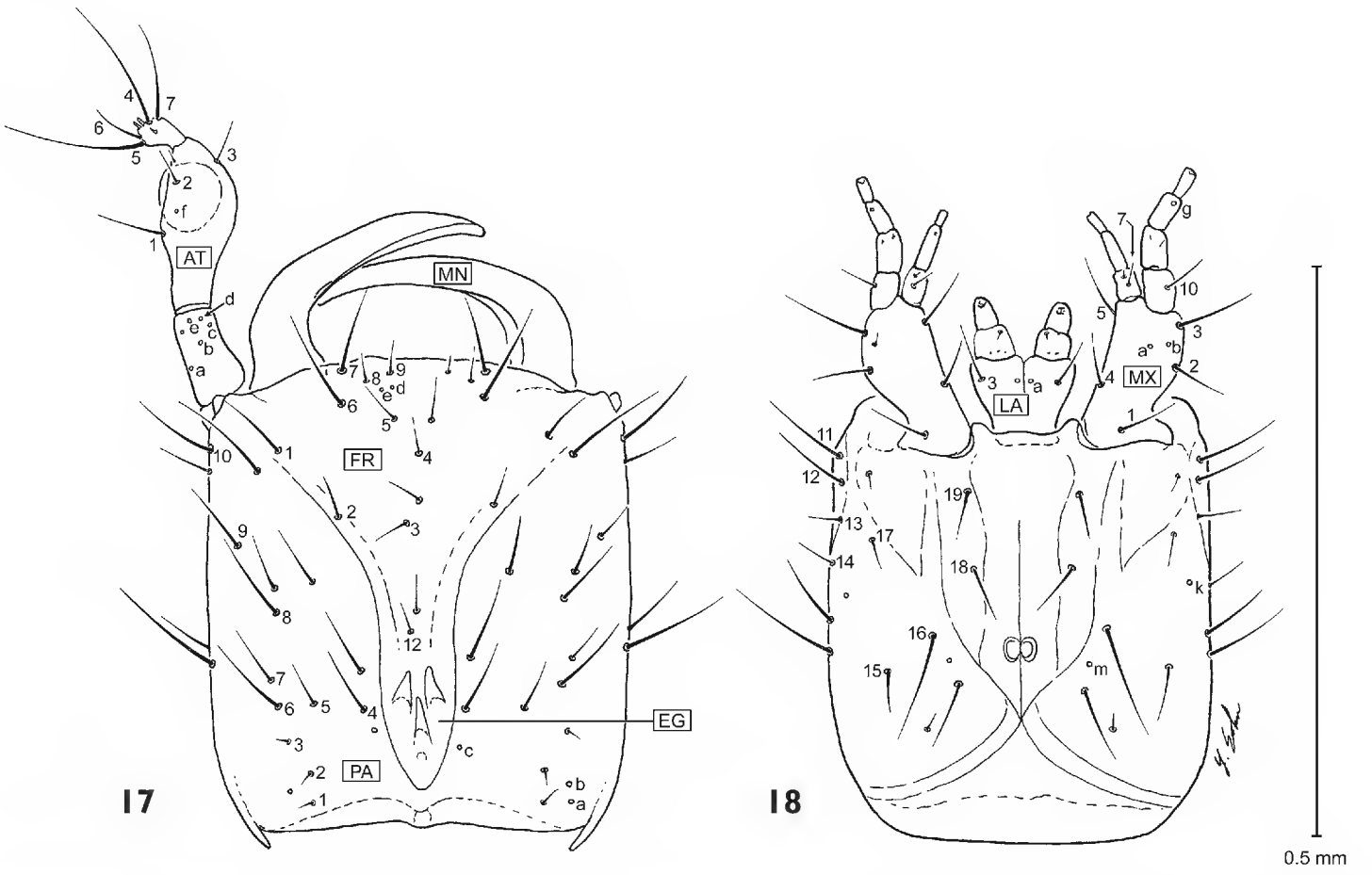
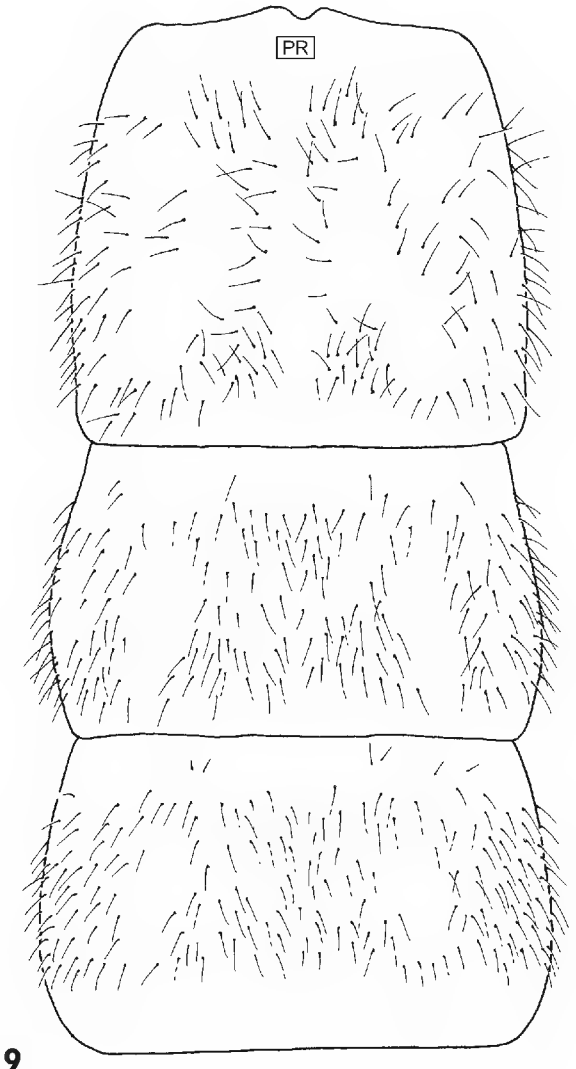


Figure 16. Habitus (left lateral aspect) of *P. aequinoctialis*, first instar; legs not shown.



Figures 17-18. 17 Head (dorsal aspect) of *P. aequinoctialis*, first instar; ventral mouthparts and right antenna not shown. **18** Head (ventral aspect) of *P. aequinoctialis*, first instar; mandibles and antennae not shown.

Legs. (Fig. 25) All legs stout, similar in proportions and setation; anterior leg slightly shorter than middle and posterior ones. Coxa with 7 setae (ancestral CO10 – CO17, with CO1-9 absent, and no pores. Trochanter with 5 setae (TR2 – TR5, and TR8) and one pore. Femur with 4 setae (FE2 – FE5) and no pores FEa and FEb. Tibia with 7 setae (TI1 – TI7) and no pores. Tarsus with 1 constant seta (TA1) and no pores. Claws simple, with no setae or tooth, symmetrical in shape and size.



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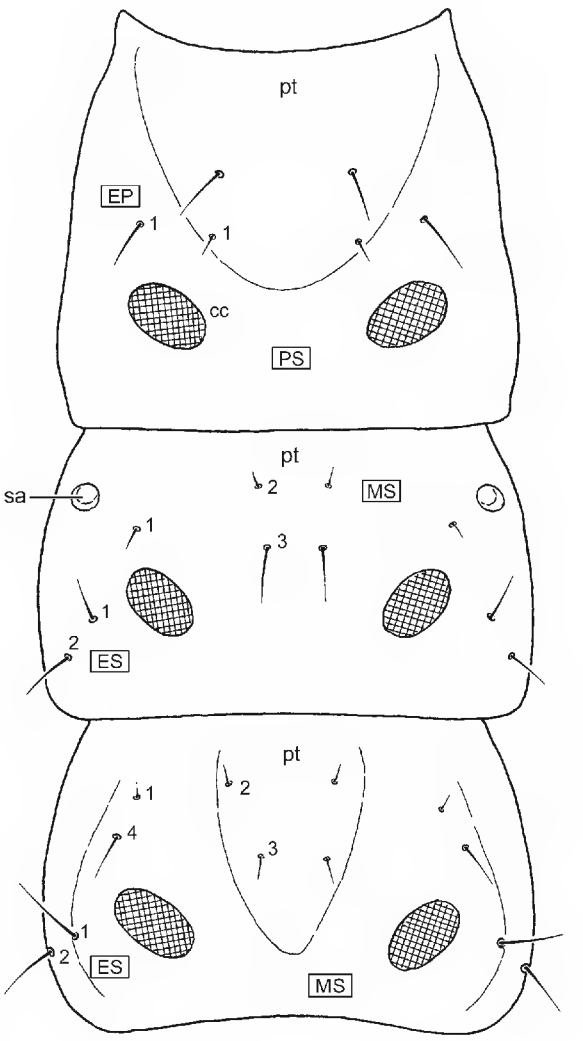

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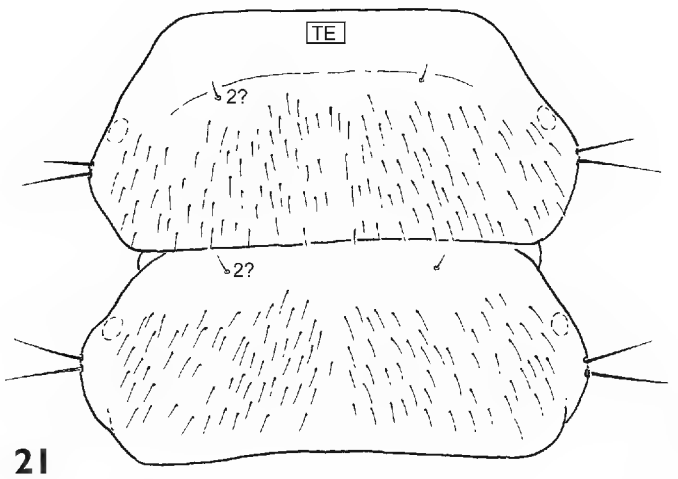

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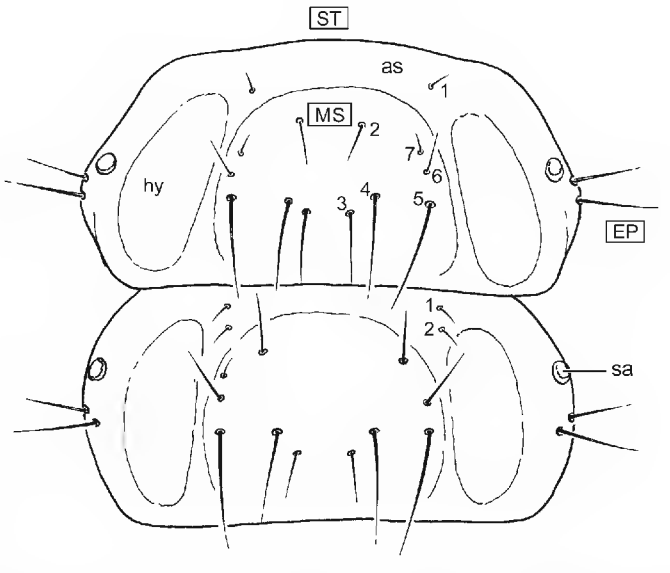

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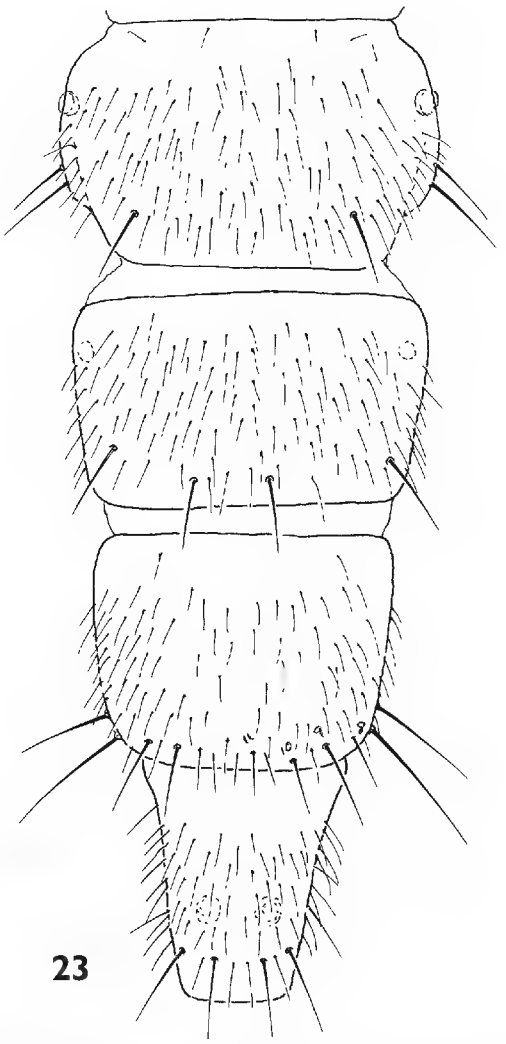
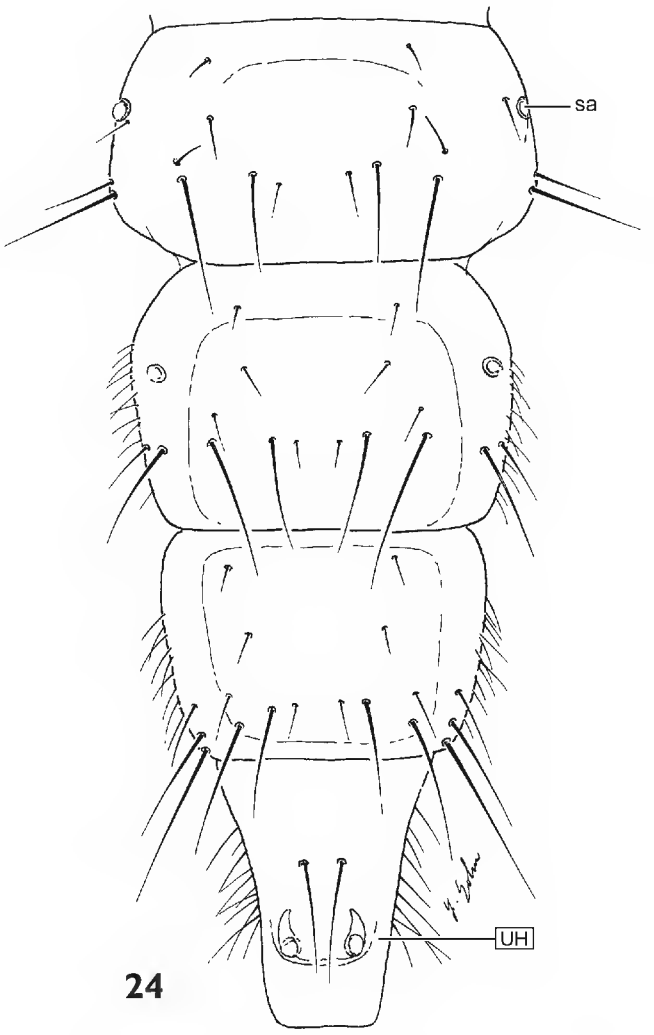
Figures 19-22. 19 Thorax (dorsal aspect) of *P. aequinoctialis*, first instar; legs not shown. **20** Thorax (ventral aspect) of *P. aequinoctialis*, first instar; legs not shown. **21** Abdominal terga I & II (dorsal aspect) of *P. aequinoctialis*, first instar. **22** Abdominal sterna I & II (ventral aspect) of *P. aequinoctialis*, first instar.





Figures 23-24. 23 – Abdominal terga VII to X (dorsal aspect) of *P. aequinoctialis*, first instar. **24** – Abdominal sterna VII to X (ventral aspect) of *P. aequinoctialis*, first instar.

Instar II. Form. (generally as in Fig. 35) Hypermetamorphic stage 2 instar.

Coloration. White; head capsule creamy-white with mouthparts slightly infuscated in part; mandibles piceous at tips.

Chaetotaxy. *Head.* (Figs. 26-27) Frontale (Fig. 26) with 7 "ancestral" setae (FR1 – FR7), and no pores. Parietale (Figs. 26, 27) with 12 setae (PA3, PA5– PA7, PA9, PA11 – PA13, PA15 and PA17) and no pores. Antenna (Figs. 26): antennomere 1 with one "ancestral" seta (AN1) and no pores. Dome-shaped hyaline sensillum absent. Mandible (Fig. 26) falciform without setae and pores. Labium (Fig. 27) without setae or pores. Maxilla (Fig. 27): cardo without setae; stipes with 3 "ancestral" setae (MX3 – MX5), and no pores, nor variable setae (gMX) on dorsal side; lacinia (Fig. 27) without setae; galeomere without setae; palpomere 1 and 2 without setae, palpomere 3 with 2 minute apical setae, no pores.

Thorax. Prothorax: Figs. 28-29. Notum (Fig. 28) with 12 major "ancestral" setae (PR2 – PR4, PR6 – PR14) and numerous auxiliary setae (not labeled), and no pores on each side. Epimeron, episternum, and trochantin not defined. Prosternite (Fig. 29) with a ring of auxiliary setae, gPS absent.

Mesothorax and *metathorax*: Figs. 28-29. Mesonotum (Fig. 28) with 9 "ancestral" setae (ME1 – ME2, ME8 – ME14), and no pores on each side. Mesepisternum (Fig. 28) with 1 seta (PL1) and no pores. Trochantin and epimeron not defined. Sternum

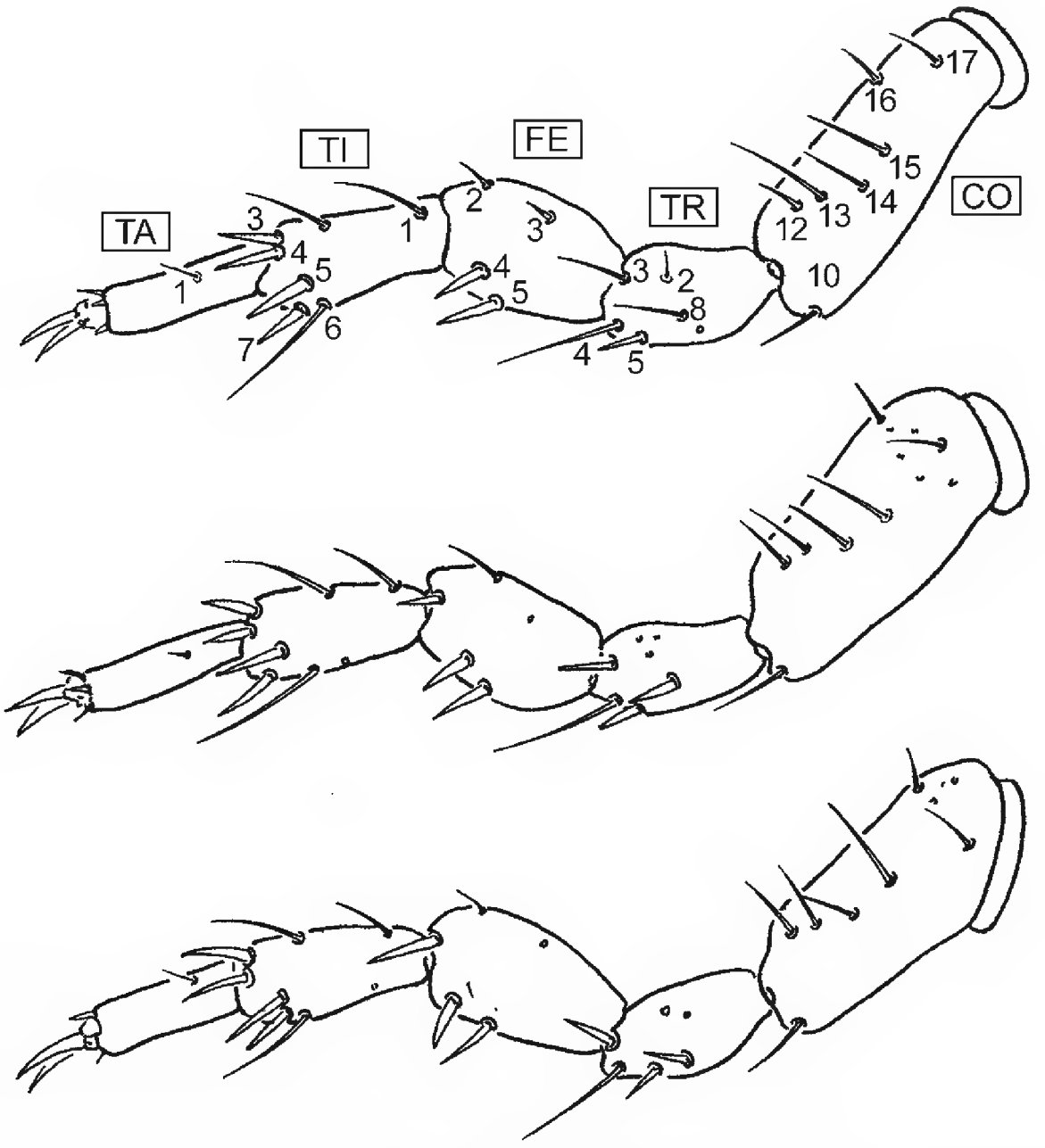
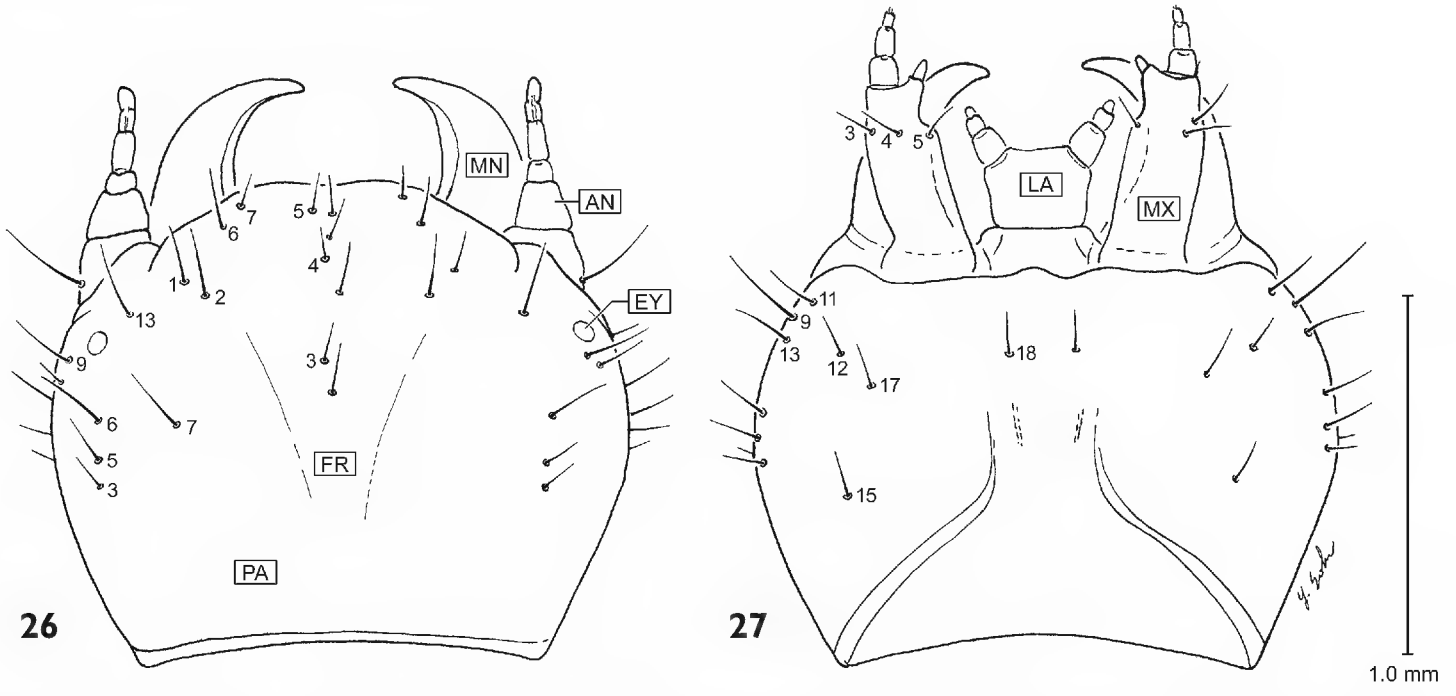


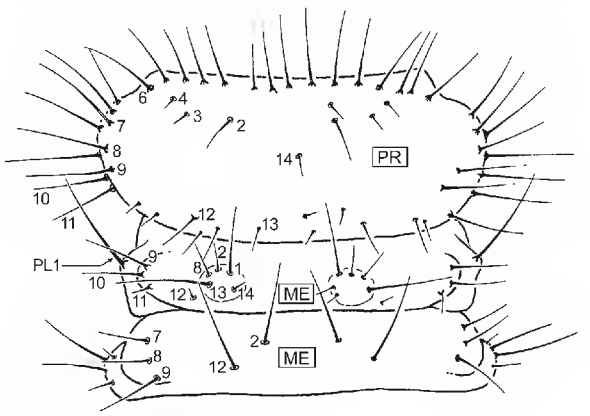
Figure 25. Legs (dorsal aspect, left side of thorax) of *P. aequinoctialis*, first instar. Top, anterior leg; middle, middle leg; bottom, posterior leg.



Figures 26-27. 26 – Head (dorsal aspect) of *P. aequinoctialis*, second instar; ventral mouthparts not shown. **27** – Head (ventral aspect) of *P. aequinoctialis*, second instar; antennae not shown.

(Fig. 29) with 9 setae (unlabeled) in a median rosette. Metanotum (Fig. 28) with 5 "ancestral" setae (MT2, MT7 – MT9, MT12), and no pores on each side. Metepisternum (Fig. 29) with 5 setae (unlabeled) and no pores. Trochantin and epimeron not defined. Sternum (Fig. 29) with 14 setae (unlabeled) in a median rosette.

Abdomen. Figs. 30-34. Tergite I (Fig. 30) with 11 "ancestral" setae (TE1 – TE11) and 5 auxiliary setae (not labeled), and no pores each side. Tergites II – VIII as in Tergite 1 with numerous auxiliary setae. Sternum with numerous setiferous rosettes. Tergite IX, X and urogomphi (Fig. 32), all with numerous setae in raised rosettes or on raised lobes, and no



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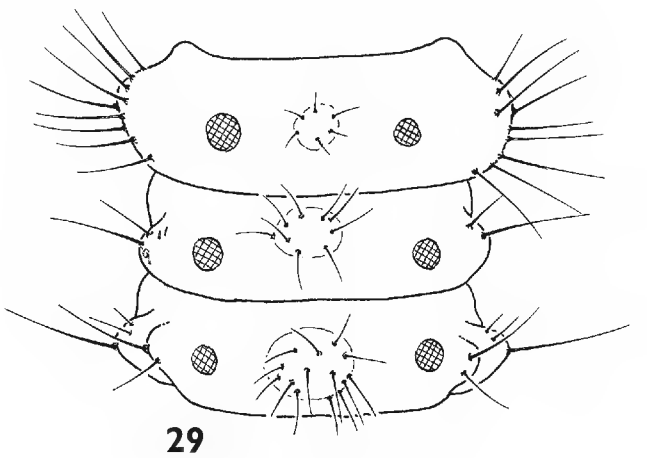

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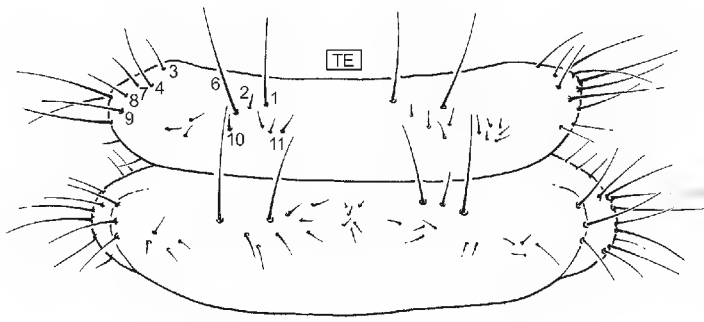

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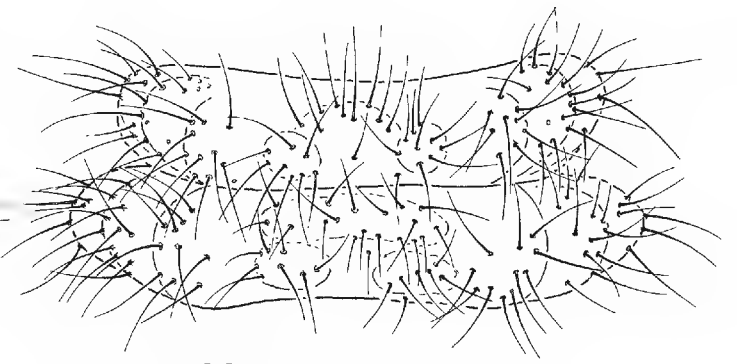

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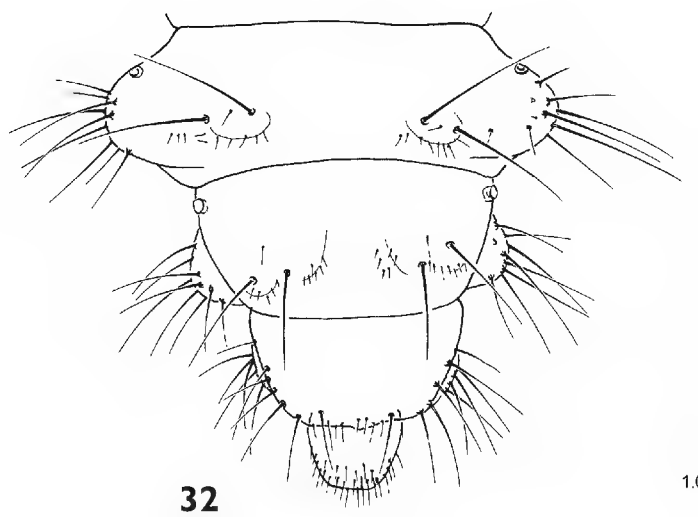

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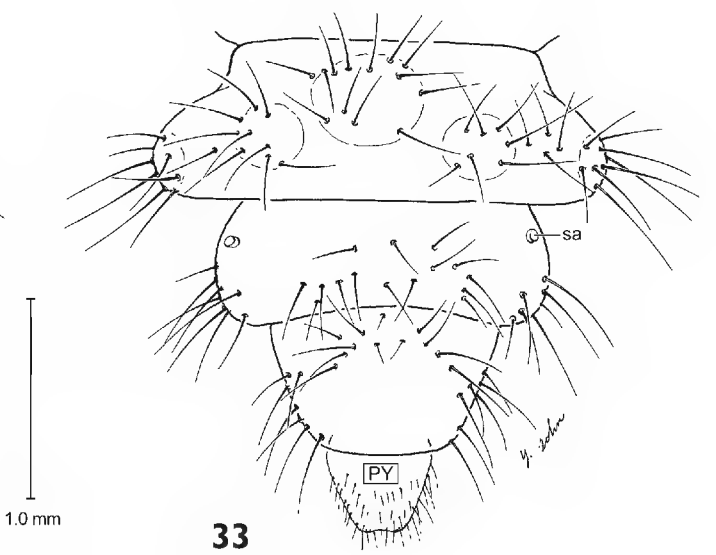


1.0 mm

33

Figure 28-33. 28 – Thorax (dorsal aspect) of *P. aequinoctialis*, second instar; legs not shown. **29** – Thorax (ventral aspect) of *P. aequinoctialis*, second instar; legs not shown. **30** – Abdominal terga I & II (dorsal aspect) of *P. aequinoctialis*, second instar. **31** – Abdominal sterna I & II (ventral aspect) of *P. aequinoctialis*, second instar. **32** – Abdominal terga VII to X (dorsal aspect) of *P. aequinoctialis*, second instar. **33** – Abdominal sterna VII to X (ventral aspect) of *P. aequinoctialis*, second instar.

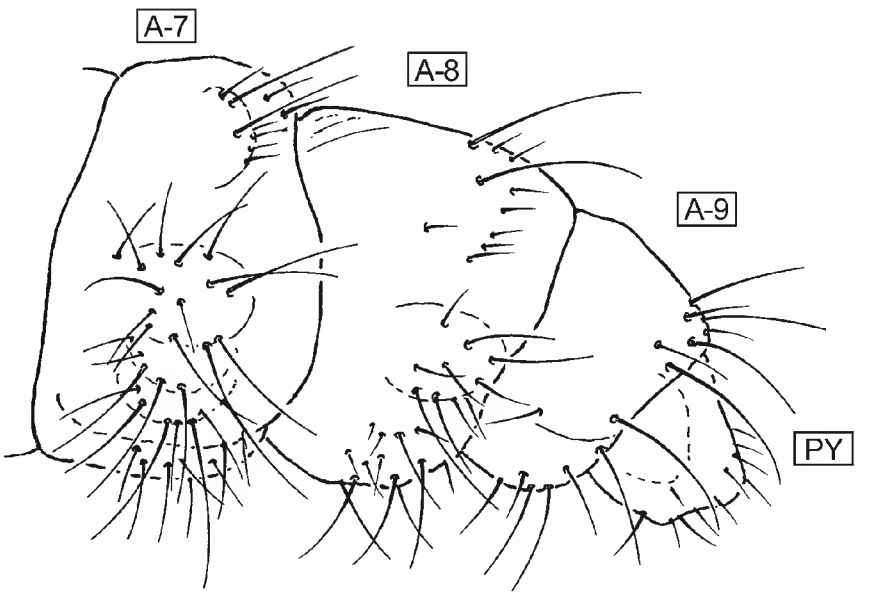


Figure 34. Abdominal sterna VII to X (left lateral aspect) of *P. aequinoctialis*, second instar.

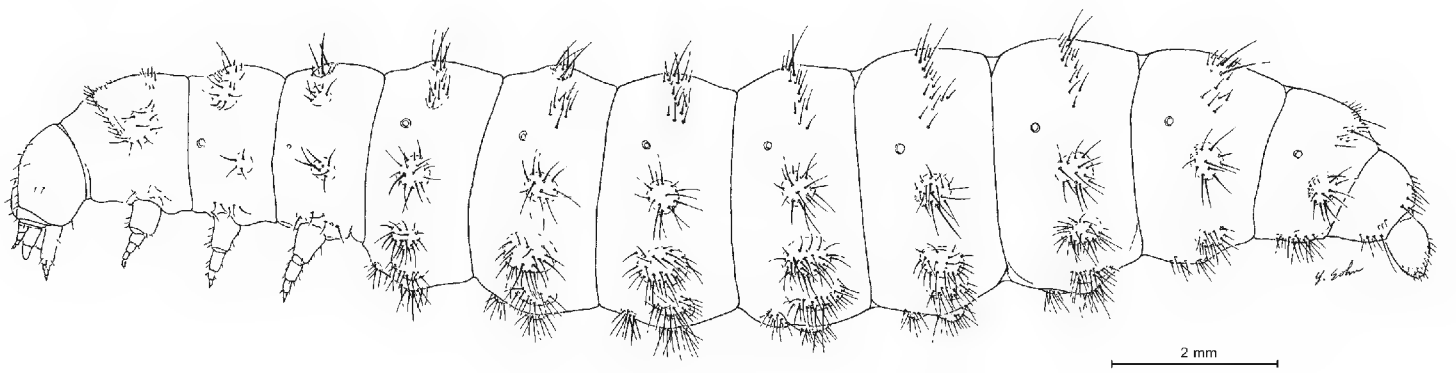
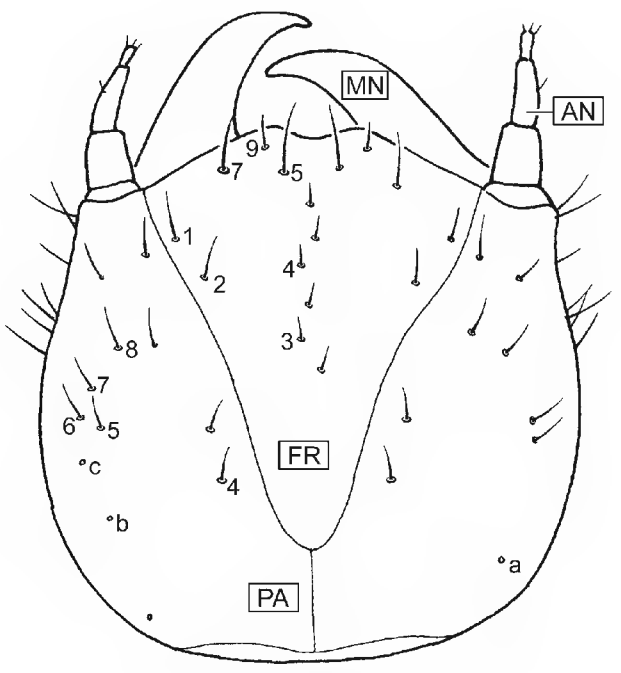


Figure 35. Habitus (left lateral aspect) of *P. aequinoctialis*, third instar; legs shown.



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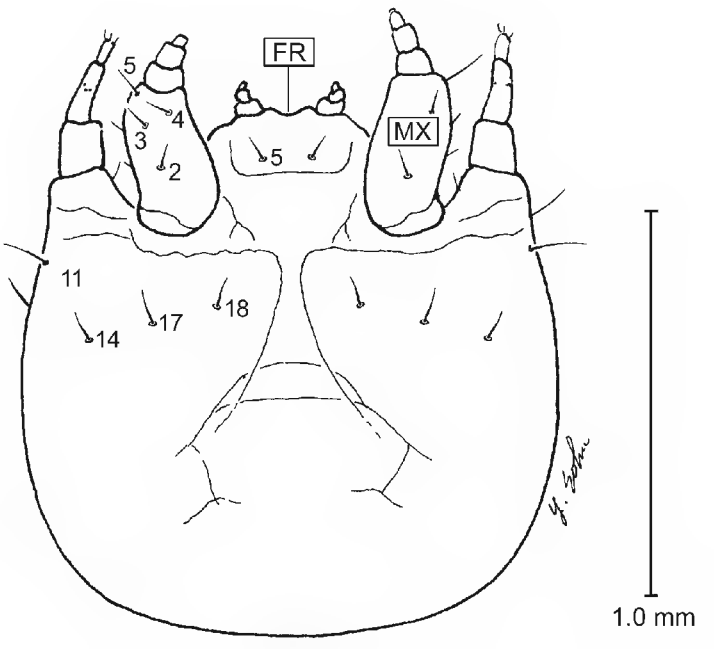

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Figures 36-37. 36 – Head (dorsal aspect) of *P. aequinoctialis*, third instar; ventral mouthparts not shown. **37** – Head (ventral aspect) of *P. aequinoctialis*, third instar; antennae shown.

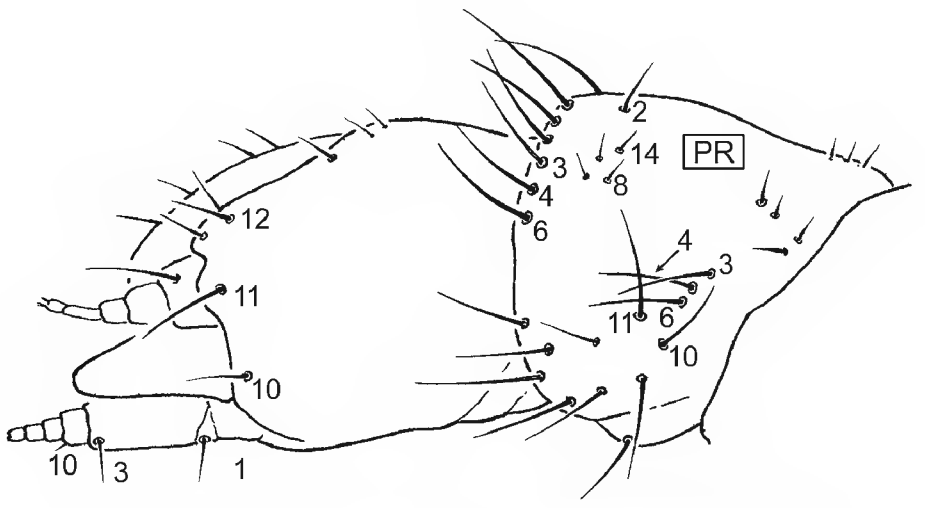


Figure 38. Head and prothorax (left lateral aspect) of *P. aequinoctialis*, third instar.

pores. Epipleurites (Fig. 33) with numerous setae and no pores. Hypopleurite not defined. Segment VII sternite (Fig. 33) with numerous setae in rosettes and no pores. Segments VIII and IX with numerous setae (not in rosettes) each side and no pores. Segment X (PY) sternite (Fig. 33, 34) with numerous auxiliary setae in apical 2/3rd, with no pores.

Legs. As in Fig. 35; reduced size and setation compared to instar I.

Instar III. Form. (Fig. 35) Hypermetamorphic stage 3 instar.

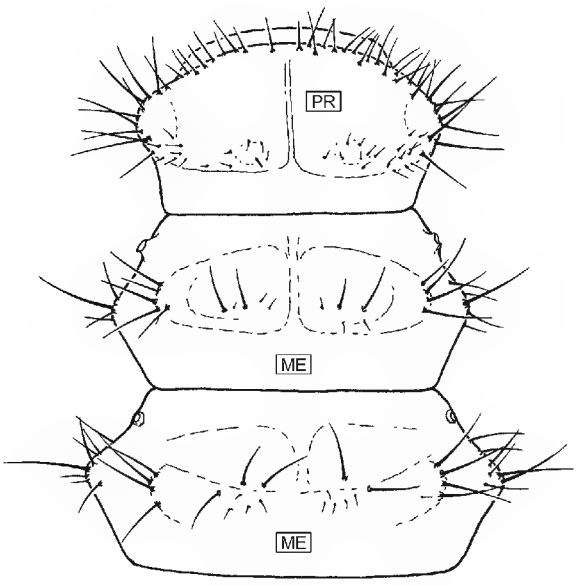
Coloration. White; head capsule creamy-white with mouth parts slightly infuscated in part; mandibles piceous at tips.

Chaetotaxy. *Head.* (Figs. 35-37) Frontale (Fig. 36) with 9 "ancestral" setae (FR1 – FR5, FR7 and FR9) and and no pores each side. Parietale (Figs. 36, 37) with 5 "ancestral" setae (PA4 – PA8) and 3 pores (PAa – Pac) each side. Antenna (Figs. 36, 37): antennomere 3 with 1 seta (unlabeled); antennomere 4 with 3 in an apical ring; the dome-shaped hyaline sensillum absent. Mandible (Fig. 36) falciform without setae and pores. Labium (Fig. 37): prementum with 1 seta (LA5) and no pores each side; labial palpomeres reduced and without vestiture. Maxilla (Fig. 37): cardo with 1ventral seta (ca1); stipes with 5 "ancestral" setae (MX1 – MX5), and no pores and no variable setae (gMX) on dorsal side; lacinia and galeomere absent; maxillary palpomeres reduced with palpomere 1 unisetose (pa10) and without other visible sensory features.

Thorax. Prothorax: Notum (Figs. 38 – 40) with numerous long setae on front margin and numerous shorter setae posteriorly (not labeled), and no pores on each side. Parietal with 6 "ancestral" setae (PR2 – PR4, PR6, PR8, PR14) and numerous auxiliary setae (not labeled), and no pores on each side. Epimeron (Fig. 38) with 5 setae (EP3 – EP4, EP6, EP10 – EP11), and no pores on each side. Episternum and trochantin not defined. Prosternite (Fig. 40) with numerous medial auxiliary setae some in a rosette, gPS absent.

Mesothorax and *metathorax*: Notum (Figs. 38, 39) with 2 long setae medially and 3 shorter setae nearby (not labeled), and no pores on each side. Episternum (Fig. 38) with numerous stout setae and no pores. Epimeron and trochantin not defined. Sternum with rosette of setae medially (Fig. 39).

Abdomen. Figs. 41 – 44. Tergite I (Fig. 41) with 2 stout setae medially and numerous shorter auxiliary setae in patches (not labeled), and no pores each side. Tergites



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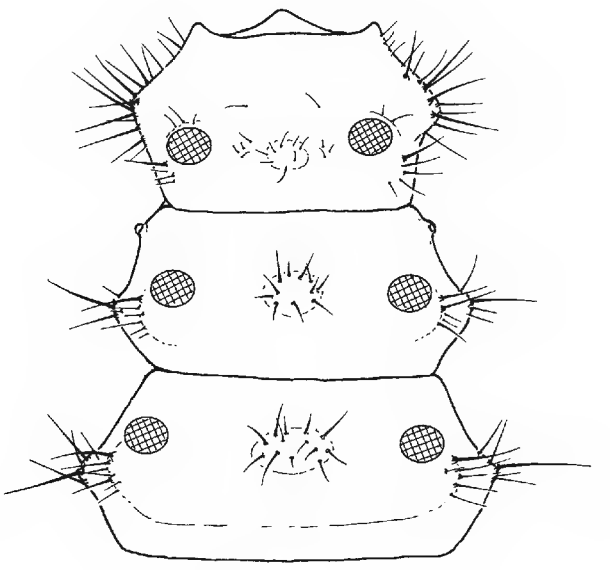

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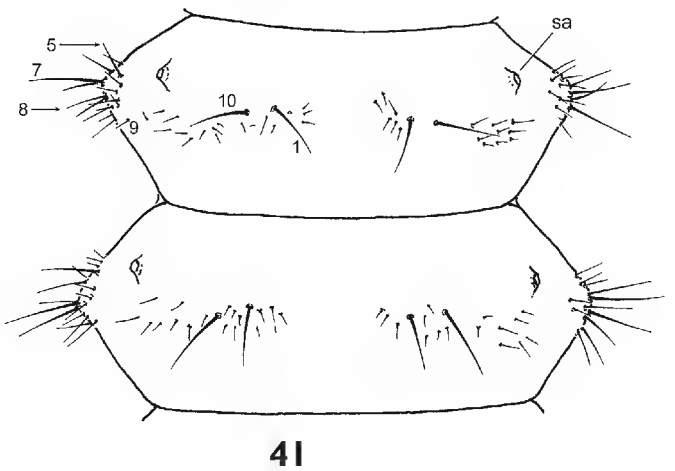

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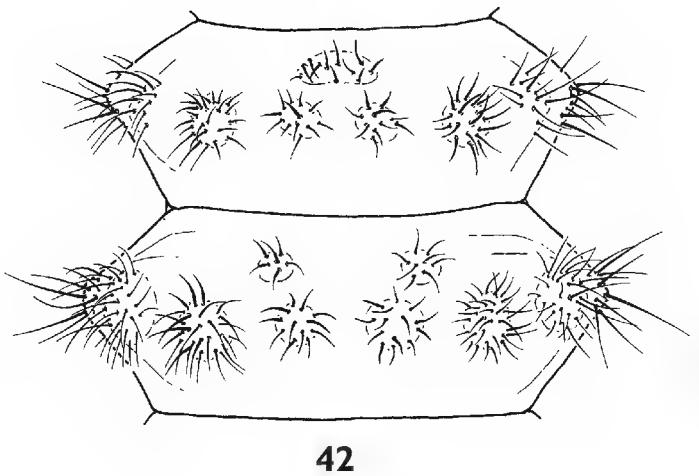

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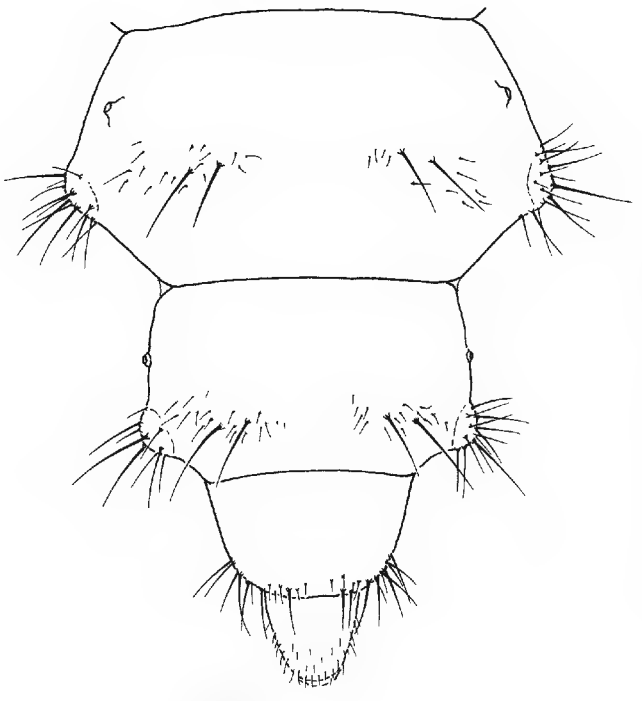

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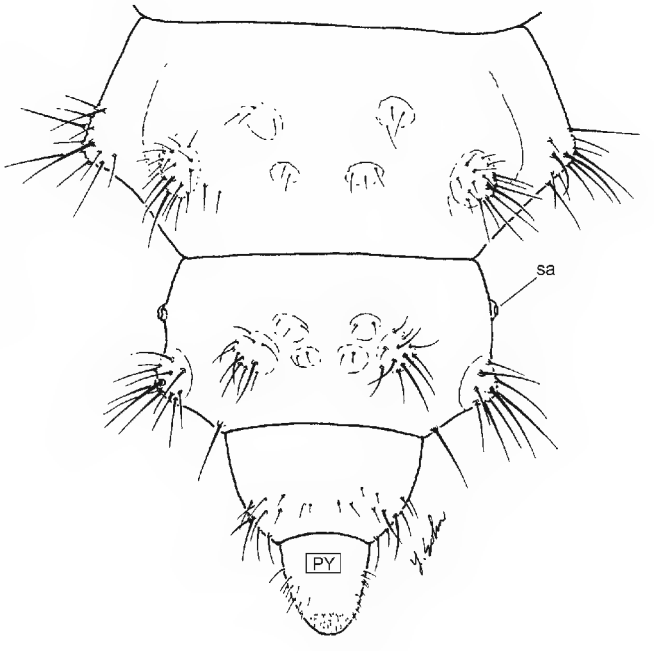

44

Figures 39-44. 39 – Thorax (dorsal aspect) of *P. aequinoctialis*, third instar; legs not shown. **40** – Thorax (ventral aspect) of *P. aequinoctialis*, third instar; legs not shown. **41** – Abdominal terga I & II (dorsal aspect) of *P. aequinoctialis*, third instar. **42** – Abdominal sterna I & II (ventral aspect) of *P. aequinoctialis*, third instar. **43** – Abdominal terga VII to X (dorsal aspect) of *P. aequinoctialis*, third instar. **44** – Abdominal sterna VII to X (ventral aspect) of P. aequinoctialis, third instar.

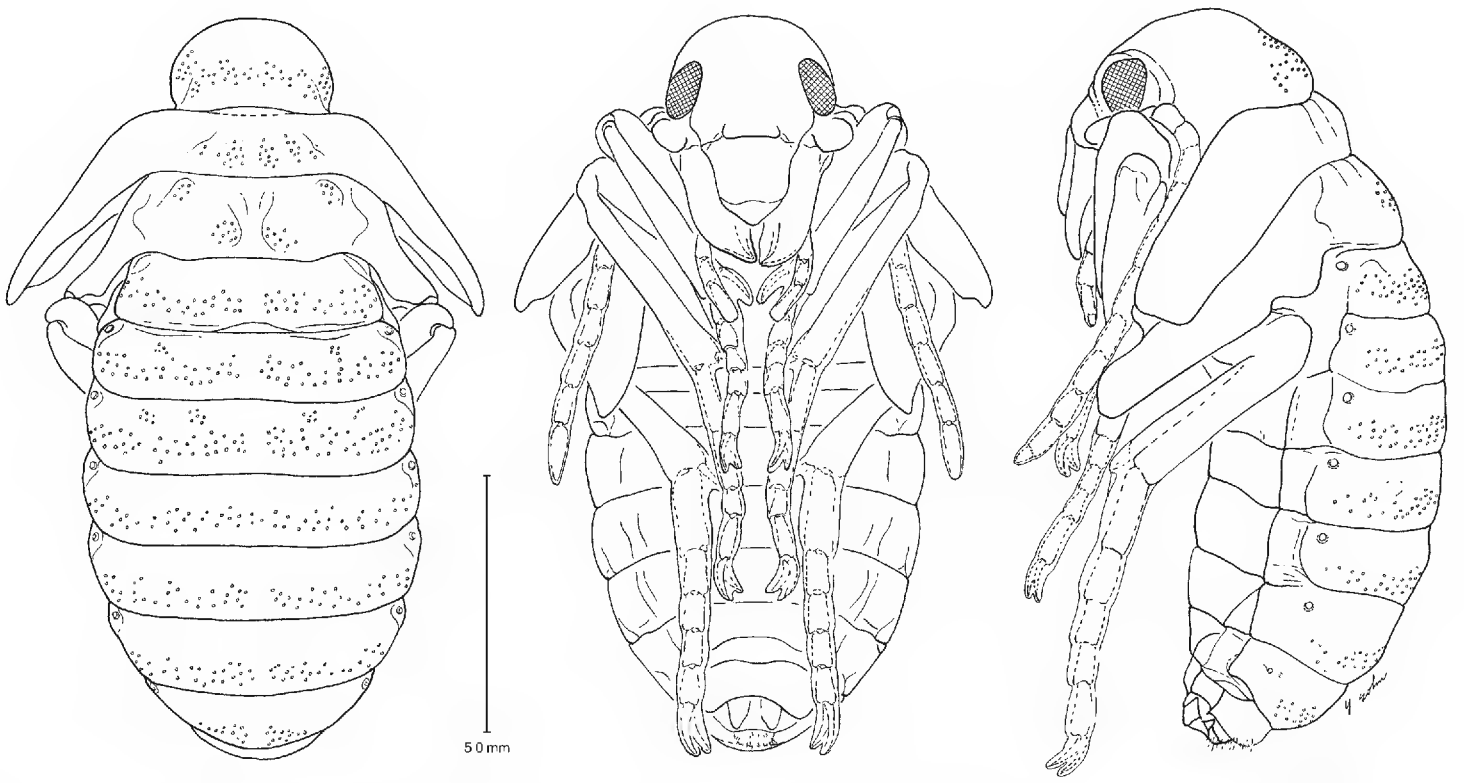

Figure 45. Pupa of *P. aequinoctialis*, dorsal (left), ventral (middle), and left (right) lateral aspects

II – VIII as in Tergite 1. Tergite IX with 2 stout setae each side and numerous shorter setae nearby. Tergite X (PY) with numerous short apical setae and no pores. Epipleurite IX (Fig. 44) with numerous long and stout setae on raised knob and no pores. Hypopleurite not defined. Segment VII and VIII sternites (Fig. 44) with numerous setae on raised knobs in rosettes each side and no pores. Segment IX sternite (Fig. 44) with subapical band of short setae each side and no pores. Segment X (PY) sternite (Fig. 35, 44) with numerous scattered short setae each side, no pores.

Legs. As in Fig. 35; reduced size and setation compared to instar I.

Pupa. Form. (Fig. 45) Typical of carabid species. In addition, pygidium with fine short setae and dorsal surface with an array of small tubercules.

Notes on advancing an understanding of phylogenetic relationships. Much works still needs to be done in solving to infer the relationships between the Brachininae tribes Crepidogastrini and Brachinini and the subtribes Brachinina, Pheropsophina, and Masticina (Erwin 1970). Here we have added larval traits that will, in part, add information toward a more robust phylogenetic analysis in the future. Immature stages of Crepidogastrini and Masticina are, as yet unknown, and we do not even know whether they are ectoparasitoids, or specialized predators. Likely, they are one or the other, but on what taxa? Larvae of *Brachinus* develop in 5 instars; they also have 6 eye-spots (as in other carabids), whereas Pheropsophina larvae have 3 instars and at most a single eye-spot, usually none. First instar *Brachinus* have no egg burster and chew their way out of the egg (Erwin 1967); *Stenaptinus* larvae possess a single-toothed egg burster; those of *Pheropsopus* have a triple-toothed egg burster. Pheropsophina larvae have pygidial hooks that aid them in attacking mole cricket egg clutches (Habu and Sadanga 1969), whereas *Brachinus* larvae do not. Larvae of *Stenaptinus* and *Brachinus* possess urogomphi whereas those of *Pheropsophus* do not.

Conclusion and discussion

Adult *P. aequinoctialis* and many *S. jessoensis* burrowed in sand-filled containers in the laboratory. Many *S. jessoensis* ~ 91.4%) but few *P. aequinoctialis* ~ 16.7%) were active on the surface in daylight. This supports field observations that *P. aequinoctialis* adults are active nocturnally. Very few *P. aequinoctialis* adults (1.2%) found brown paper towel on the sand surface to be as adequate a refuge as their burrows; perhaps more solid objects (as a result of photoperception or thigmoperception) would have been more acceptable as refuges. In contrast, more *S. jessoensis* adults (78.7%) sheltered under paper towel in daylight than sheltered in burrows, but most did not shelter at all. There is a clear contrast between the mainly diurnal behavior of *S. jessoensis* and the mainly nocturnal behavior of *P. aequinoctalis*. Timing of daily activity will have an effect on ability to find food.

All diets presented to these adults were consumed, but we did not observe cannibalism by adults. Larvae of *T. ni* alone sustained adult *S. jessoensis* of unknown age for an average 12 months. Earlier authors showed that a broad diet of animal food is acceptable to them, and neither we nor previous authors tested acceptability of plant food alone. A diet of mealworm pupae, oatmeal and raisins was avidly fed upon by adult *P. aequinoctialis*, and sustained them well, so they will feed on plant food, supporting an observation of feeding upon palm fruits in nature (Reichardt 1971). We did not attempt to produce an optimal diet for adults of either species. Adults of the two species produced many eggs on the diets provided. Females of both species oviposited abundantly on crumpled, moist, brown paper towel under highly artificial conditions. Chemicals produced by eggs or adults of mole crickets are not necessary to stimulate abundant oviposition. However, Weed and Frank (2005) found that more eggs were laid in tunnels excavated by mole crickets than in artificial tunnels, suggesting that perhaps allomones produced by adult mole crickets are detected by female *P. aequinoctialis* and influence placement of eggs.

Adult *P. aequinoctalis* oviposited in all months of the year; and adult *S. jessoensis* oviposited in most months of the year in the laboratory. Seasonality of oviposition in the field is mutable under laboratory conditions. We suspect that neonate larvae of both species suffer high mortality because they fail to detect suitable prey and thus die. Although *P. aequinoctialis* and *S. jessoensis* are highly fecund, Thiele (1977) gave examples of high fecundity among other carabids without such a specialized life cycle. Fertility of laboratory-produced *P. aequinoctialis* eggs varied for unknown reasons, at some times being very low. The evolutionary consideration is: Why are so many infertile eggs produced? Presence of two species of *Wolbachia* (Bacteria: Rickettsiae) in our 1992 *P. aequinoctialis* stock from Bolivia has been demonstrated. A suggested heat-treatment to eliminate the *Wolbachia* resulted in mortality of some adults, temporarily reduced oviposition, and failed to eliminate production of infertile eggs. The heat treatment may, of course, have killed some essential flora in the digestive system. Incubation of fertile eggs of *S. jessoensis* took 11.4 days and of *P. aequinoctialis* 13.5 days on average.

Most neonate larvae of *S. jessoensis* and *P. aequinoctialis* died when presented with mole cricket eggs in Petri dishes. They wandered for days until they died, almost continually in motion. Neonate larvae were presented with alternative diets including *A. domesticus* and

Gryllus sp. eggs, eggs and pieces of larvae of *T. ni*, intact pupae of *T. molitor*, and pieces of cucumber. All neonate larvae of both species died when presented with any diet other than mole cricket eggs although imbibition of fluid was observed from pieces of cucumber. However, a few began to feed on mole cricket eggs. Those eggs were of *Scapteriscus abbreviatus*, *Sc. borellii*, *Sc. vicinus*, and *N. hexadactyla*; however, replication was inadequate to determine any differences in survival success between these mole cricket eggs diets. At least it can be stated that *S. jessoensis* can survive on mole cricket eggs other than those of *Gryllotalpa*, in contrast to unsupported claims by Habu and Sadanaga (1965, 1969). Once neonate larvae began to feed, their survival to the adult stage on the same diet was highly probable. Perhaps larvae will not begin to feed until they encounter enough eggs to complete their development (Habu and Sadanaga 1965, 1969), but we have no data to support this claim. Faced with the impasse that neonate larvae would seldom develop on a diet of mole cricket eggs in a Petri dish, even when that dish was enclosed totally with aluminum foil to exclude light, we adopted a variant of the rearing method proposed for *S. jessoensis* by Habu and Sadanaga (1969). Using this method, an artificial mole cricket egg chamber is made in sand in a plastic vial, stocked with 30 mole cricket eggs, covered with sand, and a neonate larva is dropped onto the sand surface. The larva burrows down to enter the chamber and begins feeding on eggs. This resulted in high survival of larvae and pupae to the adult stage, and became our standard rearing method. Feeding and development seldom occurred in the more artificial conditions of a small Petri dish with mole cricket eggs piled onto a disc of paper towel, even in the dark, but we ran many feeding trials under those circumstances. Unfortunately, the method of an artificial egg chamber excluded frequent observation. Much later, we found by accident that the artificial egg chamber did not need covering with sand to exclude light. Then, we conducted more feeding trials and confirmed that *Acheta domesticus* eggs, *Tenebrio molitor* pupae, and pieces of cucumber are not acceptable diets.Adult *P. aequinoctialis* are scavengers and generalist predators. Larvae, however, so far as determined, are specialist predators on mole cricket eggs. They can develop under laboratory conditions on a diet containing only eggs of *Scapteriscus abbreviatus*, *Sc. borellii*, *Sc. vicinus*, or *Neocurtilla hexadactyla* but none survived using any other diet tried. Proof of restriction of the larval diet still is inadequate.

Each larva of the carabid genus *Brachinus* (*Neobrachinus*) feeds on only one water beetle pupa and is an ectoparasitoid (Erwin 1967, 1979) replacing its host in a small mud chamber constructed by the water beetle larva. In Europe, *Brachinus* s. str. larvae feed on the pupal stage of the carabid genus *Amara* (Saska and Honek 2004). However, each larva of *P. aequinoctialis* and *S. jessoensis* requires tens of mole cricket eggs as food to complete its development. Such behavior is more aptly termed predation (Van Driesche and Bellows 1996, p. 21 citing many earlier authors), so we consider *Pheropsophus* and *Stenaptinus* larvae to be specialist predators. At no time in our laboratory cultures did more than one *P. aequinoctialis* or *S. jessoensis* larva survive long on a single cache of eggs, so we believe they practice fratricide as has been noted in *Brachinus* (Juliano 1984). Erwin (1967) noted that fratricide did not occur in *Brachinus pallidus*, rather the first larva that began feeding became the "owner" of the pupa and the other larvae departed in search of another pupa. These larvae, when offered a fresh pupa, developed to the adult stage.

Implications for biological control

The studies reported above were initiated because of a suspicion by T.L. Erwin that *Pheropsophus* spp. larvae might, as had been reported for *Stenaptinus*, develop only on a diet of mole cricket eggs. It was eggs of invasive species of the South American mole cricket genus *Scapteriscus* in the southern USA that were the target of our studies. These studies were initiated by J.H. Frank in the name of the University of Florida/ Institute of Food and Agricultural Sciences' Mole Cricket Research Program (Walker 1985; Frank and Walker 2006). Early mention of the studies was made by Hudson et al. (1987). Prey specificity of these beetle larvae was important because the native North America mole cricket *Neocurtilla hexadactyla* was not a target. Might the South American *Pheropsophus* be adapted to South American *Scapteriscus* mole crickets but the Old World *Stenaptinus* be adapted to the largely Old World genus *Gryllotalpa*?

Habu and Sadanaga (1965) stated that *S. jessoensis* larvae feed only on eggs of *G. africana* Palisot de Beauvois. They provided no evidence that they had experimented with other diets. However, *G. africana* does not occur in Asia, and the species of mole cricket encountered by those authors may have been *G. orientalis* Burmeister (Townsend 1983). We had no access to eggs of *Gryllotalpa.* By 1987, we had found that larvae of *S. jessoensis* and *P. aequinoctialis* would develop on a diet of eggs of *Neocurtilla* (Gryllotalpinae) or *Scapteriscus* (Scapteriscinae) mole crickets but, because of difficulties in getting neonate larvae to initiate feeding, we had conducted scores of failed trials with these and other diets.

Little that we had studied pointed to need for chemoperception. Adults laid eggs abundantly on paper towels. Neonate larvae may have used chemoperception to detect that mole cricket eggs are food, but there was no evidence that such detection occurred except in a pit in sand.

The Mole Cricket Research Program then concentrated on other biological control agents, which were successful, until its funding was 'unearmarked' in 1991 (Frank and Parkman 1999). At this devastating event, to save expenses and because *S. jessoensis* clearly could not be a specialist of *Scapteriscus* mole crickets, cultures of both species were terminated.

A culture of *P. aequinoctialis* was reinitiated with stock from Bolivia in 1992. One reason was that an additional biological control agent that could be used in the vicinity of water bodies, on their banks in particular, could be beneficial in integrated pest management because application of chemical pesticides is prohibited from use in such habitats. A second reason is because of egg-guarding behavior by female *Neocurtilla hexadactyla*. These excavate two side-by-side underground cells, one of which receives the eggs, the other serves as a resting site for the female, from which she emerges fom time to time to tend the eggs (J.H. Frank and R.C. Hemenway, obs.). In contrast, each *Scapteriscus* spp. female excavates only one cell and then, after oviposition of a clutch of eggs, leaves and blocks the entrance to the cell (J.H. Frank and R.C. Hemenway, obs.). It might therefore be possible for female *N. hexadactyla* to detect and kill intruding bombardier beetle larvae. If this can be demonstrated in the laboratory, it might justify release of *P. aequinoctialis* in Florida.

Research will not be complete until the subject of egg-guarding by *N. hexadactyla* females is adequately investigated. A major problem is that we have not devised a robust method for culturing *N. hexadactyla*. Survival of adults and nymphs was poor, perhaps because the diet we used was inadequate. We observed that females move their eggs when they are disturbed, which we believe to be a previously unreported facet of their presocial behavior.

Finally, some objection might be made to the release of a beetle whose adults are scavengers and generalist predators, even though this habit is shared with adults of many other insects, including adults of the ~ 18 native species of *Brachinus* bombardier beetles in Florida. Still, population sizes must be limited by availability of mole cricket eggs, and we now have some idea of the quantity of food (≤ 2.3 large *T. ni* larvae per day) consumed by pairs of adult beetles.

Acknowledgments

Most of the work described here was supported by funds earmarked by the Florida Legislature for mole cricket research at the University of Florida in 1978-1991 (the UF/IFAS Mole Cricket Research Program). Earmarking was withdrawn (but the program was not de-authorized) after three biological control agents had been released and established in Florida, but before research on them, let alone *P. aequinoctialis*, which has not been released, was complete. Thomas J. Walker (Entomology and Nematology Dept., Univ Florida), supplied *Gryllus* sp. eggs. Fred Adams, USDA-CMAVE laboratory (Gainesville, FL) supplied *T. ni* eggs and larvae. A. Jeyaprakash (Entomology & Nematology Dept., Univ. Florida) investigated and confirmed the presence of *Wolbachia* in *P. aequinoctialis* adults. Harold A. Denmark (Florida Dept. of Agriculture and Consumer Services, Division of Plant Industry, now retired) identified to generic level a parameg-istid mite from *P. aequinoctialis*. Aquiles Silveira-Guido (Montevideo) was contracted to supply specimens and information. Karl Zinner (São Paulo) exchanged specimens of *P. aequinoctialis* for specimens of *S. jessoensis*. Herein is the background to a species of *Rhabditis* described as new by Smart and Nguyen (1994). Young Sohn provided the illustrations of the immature stages and Karolyn Darrow assembled the illustration plates; both individuals are members of the Department of Entomology at the Smithsonian Institution. Paul E. Skelley (Florida State Collection of Arthropods) provided the scanning electron micrographs of the eggs. We thank Robert McSorley and Frank Slansky, Jr. (Entomology & Nematology Dept., Univ Florida) for manuscript reviews.

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